EVOLUTION OF SEX IN PLANTS

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By

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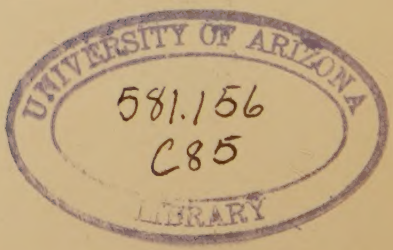

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CHAPTER I

ASEXUAL REPRODUCTION

In any discussion of the evolution of sex it is necessary to consider asexual reproduction. The extent to which asexual reproduction occurs among plants is probably not fully appreciated. In many of the lower thallophytes sexual reproduction is unknown, and in all plants exhibiting it there are also asexual methods of reproduction. It is probably true, taking the plant kingdom as a whole, that the multiplication of individuals is greater by asexual than by sexual methods. It is obvious, therefore, that sex is not an essential feature of reproduction. Historically it was the last method of reproduction attained among plants, and when it appeared it did not replace the older methods, but was added to them.

The significance of sex, therefore, is not to secure reproduction, but to secure something in connection with reproduction that the other methods do not. It is necessary to keep this fact in mind in considering the origin and real function of sex. Our conceptions of sex have largely been determined by its place in the life histories of the higher animals, in which it has become the only method of reproduction. It is difficult, therefore, to think of it as having any function apart from reproduction; but among plants the sexual method has never become the only method of reproduction. Even among the flowering plants, which represent the culmination of the plant kingdom, and

which would have eliminated asexual reproduction if it was eliminated at all among plants, reproduction by tubers, bulbs, and cuttings, as well as the universal occurrence of microspores (pollen grains) and megaspores, testify to the fact that asexual reproduction is not even a declining method.

It is also among plants that the origin of the sexual method is in evidence. It did not appear as an entirely new mechanism, detached from everything that preceded it, but arose as a gradual modification of one of the asexual methods; nor did it appear at first with all the significance it attained later. This seems obvious enough, even if the significance of sex in each step of its progress cannot be explained. If sexual reproduction has arisen from asexual reproduction, it is necessary to trace the evolution of the latter, at least to the point where sex appeared. In doing this no effort will be made to specify the plants that contribute the evidence. They are sufficiently known to botanists, and would be meaningless names to those who are not botanists. The series of facts herewith presented, however, should be clear enough to all.

The use of the term "reproduction" in this discussion must be defined. Any cell that produces another one is performing the function of reproduction, but the result may be merely the growth of an individual, or the restoration of wasted tissue, or the healing of a wound. It is obvious that such results are not included in reproduction as currently understood. As ordinarily applied, and as it will be applied here, it means the production of new and independent individuals that become self-supporting.

The lowest members of the plant kingdom are individuals whose bodies consist of single cells. In these cases the individual and the cell are identical. For the benefit of those who are not biologists, it may be said that a cell is essentially an organized unit of protoplasm called a *protoplast*. The individual, therefore, in these low plants is a single protoplast whose structure is extremely complex and whose physiology is more so. In this connection there is no need to outline what is known of the structure of a protoplast, and its physical and chemical activities could not even be outlined. The significant fact for this discussion, however, is that, among the activities of the protoplast, it has the power of self-division, by means of which it divides into two new protoplasts, each like the parent (Fig. 1). The visible machinery of this division has been described in great detail, and it indicates that an exact division of every constituent of the parent protoplast is provided for, so that each one of the daughter protoplasts is a duplicate of the parent in structure and soon it becomes a duplicate in size also.

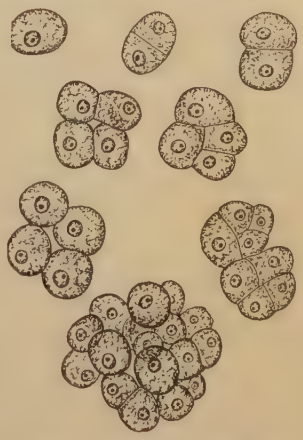

FIG. 1.—A one-celled plant (*Pleurococcus*), showing divisions resulting in new individuals.

The forces which control this machinery, and which result in making any visible machinery at all, are much more important, but they are unknown. In fact, it

is a fair question whether the so-called machinery is not made up of the visible results of an invisible process.

Whatever the mechanism of cell division may be, when the individual protoplast divides to form two new protoplasts, it performs the function of reproduction. A one-celled plant has in this way produced two new plants. It follows, therefore, that the fundamental reproductive mechanism is cell division, and there is really nothing more in the reproductive power than this phenomenon of cell division, whether it be sexual or asexual reproduction. If the essential machinery of reproduction is provided for in cell division, it follows that the cell fusion which precedes cell division, and which is often referred to as the sex act, must be regarded as an addition to the fundamental process of reproduction, an added preliminary process, not necessary to reproduction, but securing something in connection with it. In other words, reproduction is one of the functions of protoplasts, and when an individual is a single protoplast, cell division and reproduction are obviously the same.

A feature of most plant cells must be mentioned, since it is involved in the appearance of another form of asexual reproduction. In general, the protoplast is not naked, but invests itself with a firm but elastic wall or membrane. In any reproduction of one-celled plants, therefore, the wall as well as the active protoplast is divided, and new walls are formed between the two new protoplasts, thus completing the investment of the new cells. It must be remembered, however, that the wall is merely an incident in the division of the protoplast, and that wall division may be eliminated

without affecting reproduction. What may be called the first stage in the evolution of asexual reproduction, therefore, is represented by those one-celled plants whose only method of reproduction is ordinary cell division, which is a function exercised by any protoplast under appropriate conditions.

When plants become many-celled, ordinary cell division does not result in new individuals; that is, ordinary cell division and reproduction are not synonymous. The result of cell division is not new individuals, but the growth of the same individual. In other words, cell division has become a feature of growth. In this situation, therefore, the most primitive form of reproduction has come to express itself in the growth of a single individual. This transition from cell division resulting in new individuals, to cell division resulting in growth, has established, or at least has become chiefly associated with, a new form of asexual reproduction.

Before describing this, however, attention should be called to the fact that in many-celled plants certain cells may appear to have lost the power of division, while other cells have retained it. This association of protoplasts in the individual, therefore, has not only modified the form of asexual reproduction, but has resulted apparently in the loss of the power of division by certain protoplasts. An analysis of the facts may modify this impression somewhat. As a rule, a meristematic cell, that is, one that divides, usually does so when it is young. If for any reason it becomes relatively old without dividing, it seems to have lost the power, and never divides, becoming a permanent cell, as contrasted with a meristematic one. With such facts under

observation, it was natural to suggest that the power of division is a juvenile power of a protoplast, which is gradually lost as age increases. This would mean that the aging of a protoplast is accompanied by some definite physiological change; that it involves constitution as well as time. If this is true, the power of division has either disappeared or has been inhibited. That the latter alternative is the more likely is evident from the following facts. Whenever a cell becomes permanent it passes through its juvenile stage without dividing. This power, common to all young cells, has failed to express itself. Something, therefore, inhibits the division of young cells and determines that they shall become permanent, while their associates are not inhibited and continue to divide. It is also well known that in many cases a relatively old cell, fairly to be regarded as a permanent one, can regain the power of division under certain conditions. In this case an inhibition has apparently been removed from an old protoplast, just as it may be applied to a young protoplast. It becomes obvious, therefore, that the division of a protoplast is not a necessary function of its age, although it usually expresses itself in the juvenile stage. It is a power always present, which may be inhibited or may be permitted to express itself at any time in the life of an active cell. In any event, this shows that the power of reproduction is possible in any protoplast at any stage of its active life, and also that it may be inhibited at any stage.

As stated above, in many-celled plants cell division, which is the fundamental process of reproduction, results ordinarily in the growth of a single individual rather

than in new individuals, and therefore does not result in reproduction as we have defined it. This situation necessitates a new form of asexual reproduction, not in essential features, but in details. So long as cells are held together by their walls, in the continuous framework of an individual, there can be no production of new individuals. There must be detachment from the parent stock sooner or later as a preliminary to the series of cell divisions that are to result in the new individual. Among the lower algae this is accomplished in a very simple way, and the separation from the parent stock takes place at the very beginning of the new individual. The protoplast detaches itself from the cell wall, which is a part of the permanent framework of the parent plant, and escapes into the surrounding medium (Fig. 2). This escaped protoplast is the so-called *spore*, which is nothing more than a protoplast acting independently of its wall and of its parent plant. No new powers belong to the escaped protoplast; it begins a series of cell divisions, but, being free from the parent form, the divisions result in a new individual. The difference between such a spore, therefore, and any other protoplast belonging to the parent body is not a difference of power but of opportunity.

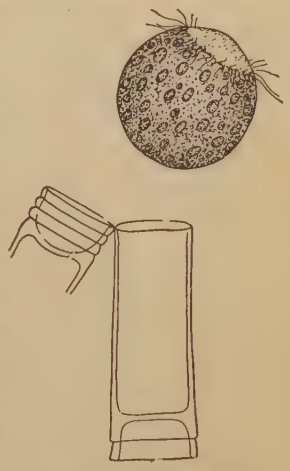

FIG. 2.—A spore of *Oedogonium* just escaped from the old cell wall.

Ordinarily the spore-forming protoplast begins a series of divisions before it escapes, resulting in several spores, each one of which, continuing the divisions, forms a new individual. It is obvious that the series of cell divisions is responsible for reproduction, whether the protoplast divides before it escapes or escapes before it divides. The number of spores is a detail of secondary importance, and the relation of these spores to the medium (water or air) is also a secondary matter. If they escape into water they are likely to develop swimming appendages (*cilia*); if they escape into air they develop a protective wall. In this connection attention might be called to cases among the fungi in which the detachment of spores is secured, not by the discharge of protoplasts, but by the abstriction of walled cells from special branches. This pinching off a part of the body is merely a detail of separation. The essential fact is that a spore means a protoplast separated from one individual and capable of producing another individual.

The multitude of names applied to spores on the basis of secondary characters has obscured the fundamental idea that belongs to all of them. The ordinary definition of a spore is that it is a single cell, specially "set apart" to reproduce. It is not necessarily a single cell when it escapes, for any spore may begin its reproduction divisions before it escapes, nor is it specially "set apart" for this function in the sense that it is differentiated in structure and power from the other protoplasts. It is literally "set apart," that is, detached from the parent stock, and that seems to be the only reason why it reproduces and the other protoplasts do not.

Although spore-formation is an effective method of producing new individuals asexually from many-celled individuals, it should not be understood that reproduction by spores is restricted to many-celled individuals. There are one-celled plants that also have spores, which means that for some reason the protoplast under certain conditions begins a series of divisions that do not involve the wall. It cannot be said, therefore, that spore-formation was developed in consequence of the multicellular habit of body, but that if it had not been developed, many-celled individuals could not have multiplied asexually except by fragmentation, which is simply body division that involves a group of cells.

It would be interesting to know what conditions determine the separation of a protoplast from its wall and its abandonment of a structure it had made and kept in condition. A possible suggestion may be obtained from the occasional behavior of protoplasts when protecting themselves against unfavorable conditions. Among the one-celled algae it is very common for the cell wall to become thicker in response to the influence of conditions unfavorable to vegetative activity. Upon the return of favorable conditions, the protoplast abandons the thick wall, made useless for an active cell, and forms a new wall. In other cases, as among the bacteria, in response to unfavorable conditions the protoplast becomes separated from its limiting membrane, rounds off, condenses, and passes into a dormant stage. These protected and dormant protoplasts of the bacteria are usually called "spores," but their significance is protection rather than reproduction,

and certainly they do not multiply individuals. They are the same individual in an inactive condition, no new individual being produced. In both of these cases the behavior of the protoplast is in response to conditions unfavorable to vegetative activity.

The same kind of response appears in ordinary spore-formation, in which the protoplasts become freed from the wall, round off, and are entirely detached from the general life of the individual producing them. In many algae and fungi it is entirely possible to control spore-formation experimentally. In other words, conditions can be supplied which inhibit spore-formation indefinitely, and other conditions can be supplied which stimulate abundant spore-formation. In general, whatever diminishes vegetative activity favors spore-formation, so that it is the physiological condition of the protoplast that determines whether it continues to do vegetative work or becomes a spore. It is well to emphasize this fact, because there is a general impression that spore-formation depends upon a certain amount of maturity in the plant, in other words, that plants produce spores "when the time of spore-formation comes." It is true that the time of spore-formation is measurably uniform in the history of a given plant, but this simply means that the condition of spore-formation is measurably uniform in making its appearance. If it should appear earlier or later than the usual time, spore-formation will occur in spite of the time. The suspicion is that the favorable condition that induces spore-formation experimentally is represented in nature by the waning activity of the plant. Regular periods for spore-formation furnish abundant testimony to the

remarkable uniformity of conditions in nature. It seems clear, therefore, that spore-formation is a response to relatively unfavorable conditions on the part of plants whose activity extends through a period long enough to encounter varying conditions.

One of the problems of reproduction, perhaps to be regarded as the most fundamental one, has been suggested by the previous discussion. When protoplasts are detached from a parent plant, whether it be a single protoplast called a spore, or a group of protoplasts, as in the case of a propagating bud, the whole structure of the parent is reproduced. Of course, the essential separation is physiological, which may take place although complete structural separation has not been effected. When one considers the reproductive power of any group of active cells isolated from the parent stock, such as gemmae, propagating branches, buds, tubers, bulbs, cuttings, isolated nodes, and even leaf fragments, it becomes evident that reproduction is a function of every active cell, and that it can express itself when certain conditions are supplied. The conspicuous condition seems to be detachment from the parent stock. It is really a restoration of lost parts, and therefore is a form of regeneration, differing from what is ordinarily called regeneration in degree but not in kind. From this point of view a spore is to be regarded, not so much as a specialized reproductive cell differing in power from other protoplasts, but as a single detached protoplast rather than a group of them, and therefore regenerating all the structures of the body. What induces these detached protoplasts, whether single or in groups, to produce a new individual, is no more

clear than what induces a fertilized egg to produce a similar structure, but both seem to belong to the same category, and that is a series of divisions that result in a definite structure.

A second stage in the evolution of spore-formation is the differentiation of sporangia, which at first are merely special spore-producing cells (Fig. 3). In the first stage of spore-formation described above, any active protoplast of the body is capable of becoming a spore or of dividing to form spores. In the second stage, apparently the power of spore-formation has been lost by most of the protoplasts, which still retain the power of cell division, as expressed in growth. This is usually spoken of as a differentiation of functions among the cells of the body, most of them retaining their vegetative activity and power of division, but losing their power of spore-formation; while comparatively few cells retain the power of spore-formation and are vegetatively active only so far as it has to do with their own life. It is

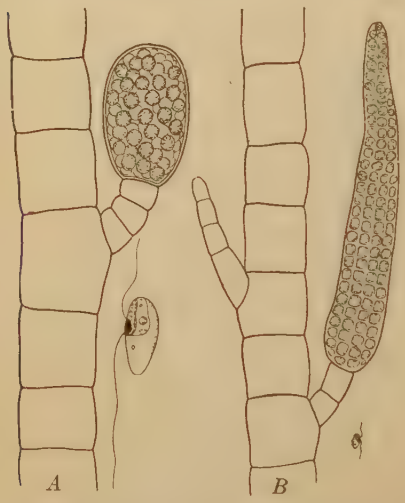

FIG. 3.—A brown alga (*Ectocarpus*): *A*, part of a filament showing a sporangium, and also an escaped spore; *B*, part of a filament showing a gametangium, and also an escaped gamete.

possible to arrange a series of algae, beginning with forms in which every protoplast is capable of spore-formation, and continuing through forms showing every degree in the restriction of this power, until finally forms are reached in which the sporangia are completely separated and distinct from the general vegetative body.

It should be remembered, however, that this differentiation of functions is still dependent upon a difference in conditions. In other words, even when there are distinct sporangia, this does not imply that spores are being formed under the same conditions that favor vegetative activity. In fact, during maximum vegetative activity, as a rule the sporangia are not formed. The conditions that favor spore-formation favor sporangium-formation. The sporangia are not formed as part of the body, awaiting appropriate conditions for spore-formation. When such conditions arise, sporangium-formation occurs whenever sporangia are distinct appendages of the body. When they are not, they are simply the vegetative cells selected to form spores. The fundamental difference, therefore, between plants without and with distinct sporangia is that in the former all protoplasts can respond to the conditions for spore-formation, while in the latter only a restricted number of protoplasts respond. What determines the selection is an important question which remains for physiology to answer.

It has been stated often that such a reproductive cell as a spore represents a cell with its primal powers, that is, powers that belonged to all cells originally; and that the other cells of the body, losing the power of

reproduction through spore-formation, have become specialized cells. It is true that if specialization consists in losing a power, and lack of specialization means retaining it, then ordinary vegetative cells are specialized and spores are not, but the vegetative cells do retain the primal power of reproduction, in that they are able to divide. Spores represent another form of expression of the reproductive power; this form of reproduction is not primal, common historically to all cells, but is new in detail.

When the differentiation of sporangia takes place first, the vegetative cells have either lost the power of spore-formation, once common to all vegetative cells, or are inhibited from expressing it. Spore-formation by cells ordinarily vegetative occurs often enough to assure us that spore-formation is only inhibited in vegetative cells. It thus appears that vegetative cells, not acting in spore-formation, have become simpler in function. On the other hand, the sporangia, separated from the ordinary vegetative activity of the body, and nourished by the body in general, produce spores which are much more highly specialized cells than the ordinary cells of the body. Their increasing complexity in structure is visible in most cases, and there is no reason to doubt that their physiological specialization is equally marked. Certainly such a cell is more frequently equipped for reproducing a more or less complex body than an ordinary cell would be. It must be remembered, however, that the difference of equipment is a difference in degree and not in kind; a greater storing of the energies to be expressed in reproduction in the one case than in the other.

The claim, therefore, is that sporangia are not merely special organs, set apart from the rest of the body and detached from the ordinary activities, but that they are differentiated not only in their ability to respond to conditions favoring spore-formation, but also in the specialization of the spores they produce. For all ordinary cells, the primary reproductive power is retained only in cell division; reproductive power becomes more highly developed when special organs are set apart to produce reproductive cells. Spores to whose development a highly complex body contributes, and which are equipped to produce a complex body, must be regarded as highly specialized cells.

A summary of what may be called the three stages in the history of asexual reproduction, as given above, can be stated as follows. The first stage is represented by cell division, which belongs to cell activity in general; in other words, it is a process as natural to all protoplasts as any work. The second stage is represented by spore-formation, in which ordinary vegetative cells, under certain conditions, produce spores. In this case the activities of a cell are differentiated by varying conditions and are not differentiated permanently. The third stage is represented by the production of spores by special cells, which are differentiated in function permanently from the ordinary vegetative cells. This specialization of certain cells is accompanied by the inhibition of the spore-producing power of cells in general, and as a result the spores become more highly specialized. Through these three stages asexual reproduction had passed before sexual reproduction became established. This does not mean that

sexual cells followed these three stages as a definite sequence, but that in connection with the evolution of spore-production the sexual cells appeared.

Before presenting the origin of sexual cells from spores, the further evolution of spore-production in connection with sexual reproduction may be considered. Among the vascular plants, a differentiation of spores occurs, related to the differentiation of sex. In the lower groups exhibiting sexual reproduction, the spores are all alike in appearance, usually producing individuals that bear the two kinds of sexual cells. In other words, such an individual is bisexual. Not infrequently the individuals produced by such spores are differentiated sexually into male and female individuals, but no differentiation of the spores producing them is observable. Among the vascular plants, however, the spores begin to differ in appearance, evidently in relation to the differentiation of sex (Fig. 4). Spores begin to be distinguished as large and small (*megaspores* and *microspores*), and apparently the only difference is that of size, although the constant difference in the product would indicate a more fundamental difference. The difference in size is due to the number of spores produced by the sporangium. In case only four spores are produced in one sporangium and hundreds are produced in another, the four spores are correspondingly larger. This great difference in size involves great difference in nutritive power, the microspores having

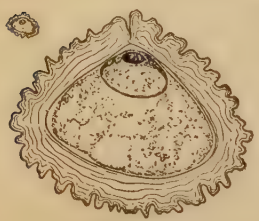

FIG. 4.—A megaspore and microspore of a club moss (*Selaginella*) drawn to same scale.

very much less than the megaspores. The significant result of this differentiation is that the megaspores produce only female individuals and the microspores only male individuals. Among plants there is a very definite relation between high nutrition and the production of the female sex organ, so that it is impossible for so small a cell as a microspore to produce a female individual. This statement is not meant to imply that the difference between the two spores is merely one of nutrition, but that whatever the fundamental difference between "maleness" and "femaleness" may be, it is obvious that the latter cannot express itself except under conditions of high nutrition. This differentiation of spores, therefore, results in a definite differentiation of sexual individuals, so that plants become distinctly and permanently male and female. In this way the two methods of reproduction have reacted upon one another, a situation which will become much clearer when the differentiation of sex is described.

A final stage in the evolution of spore-production is attained when the two kinds of spores are produced by two kinds of individuals. This is illustrated by the familiar example of the willow or the chestnut, in which one individual produces microspores and another produces megaspores, or, in ordinary phraseology, one plant bears staminate flowers and another bears pistillate flowers.

A summary of all the stages in the evolution of spore-production is as follows:

(1) The production of spores by any active cell.

(2) The production of spores by a special cell or organ (sporangium).

(3) The differentiation of spores in size, resulting in the production of male and female individuals.

(4) The differentiation of spore-producing individuals, so that the two kinds of spores are produced by different plants.

This emphasizes the fact that asexual reproduction by spores is a constant and conspicuous method throughout the plant kingdom, after plants became multicellular, and that when it came to be associated with sexual reproduction, the two reacted upon one another in the further evolution of both methods.

CHAPTER II

THE ORIGIN OF SEX

In discussing the origin of sex it must be understood that only the visible morphological structures are referred to. Even the morphology of the situation will have to be restricted to the gross aspect of the sexual cells (*gametes*). There are cytological features of gametes which cannot be accounted for historically as yet. It is also obvious that the pairing and fusing of gametes indicates a physiological situation that does not exist in spores. At the same time, the origin of the gamete as a whole seems obvious, both as to the structure from which it came and also as to the conditions under which the origin occurred. The cytological and physiological changes involved at the start are probably small as compared with those that developed later in connection with the so-called differentiation of sex. In any event, the origin of the gamete is the origin of sex, and the gross visible details of this origin will be presented.

If all plants were sexual, the origin of sex would be as obscure a problem as the origin of life. Fortunately, in the evolutionary sequence of plant groups the sexual cells appear for the first time far above the most primitive known plants, and therefore are as definitely related to previous structures as are any other features of evolutionary progress. It is evident that the gametes did not appear once for all, but that they arose independently in several plant groups, in response to similar

conditions. For example, the beginnings of sexual cells are seen among both the green algae and the brown algae, in regions of the two groups that could by no chance be related; and the same fact is true in reference to several distinctly differentiated subdivisions of these two groups. Gametes, therefore have appeared as a natural response to certain conditions, and sexuality is a product of plant evolution as natural and as distributed as is the production of spores.

FIG. 5.—*Ulothrix*, discharging spores (below) and gametes (above): above the filament are pairing gametes, and above them are two zygotes.

One of the fresh-water algae (*Ulothrix*) is commonly used to illustrate the origin of gametes, which means the origin of sex. It is no better for this purpose than many other algae, but it is a common form and is an excellent example (Fig. 5). Its body consists of a single row of cells, forming a simple filament. All of the cells are vegetatively active so long as vegetative conditions are favorable, and all of them are meristematic, the cell divisions resulting in the elongation of the filament. When the conditions become less favorable for vegetative activity, some of the protoplasts become detached from their walls and usually begin to divide. Such divisions naturally do not result in the growth of the body, but in spore-formation. The size of the spores depends upon the number of successive divisions, and in the

form referred to their number may range from one to thirty-two in different cells of the same filament. This means great variation in the size of spores, but otherwise they are alike. All of them have swimming appendages, for they are discharged into the water, but the largest ones have four cilia and the smallest ones two, while those of intermediate size develop either two or four. The number of cilia, therefore, seems to be simply related to the size of the spore producing them.

The largest spores show their character by their behavior, soon beginning to germinate, and finally producing new individuals. The spores of intermediate size also germinate, but the growth of the new individuals proceeds more slowly, as if the available amount of nutrition is not sufficient to secure vigorous and rapid growth. The smallest spores occasionally germinate, but produce very small filaments, really dwarf individuals. These spores are apparently incapable of producing individuals of normal size and vigor. In all the cases the ability to produce new individuals shows that all these cells are spores, apparently differing only in size, and this difference seems to be related to the capacity for vigorous germination. It is a temptation, therefore, to infer that the difference in size is merely a difference in nutritive capacity, and that spores may diminish in size so much through repeated divisions that they are no longer able to function as spores in producing new individuals.

The significant fact, however, remains to be told. Although the spores of smallest size seldom germinate, apparently having lost the capacity, they come together

freely in pairs, and each pair fuses to form a single cell. This fusion cell is able to germinate vigorously and produce a new individual, apparently having regained the power of a large spore. This act of fusion is the sex act, and the fusing cells are sexual cells (*gametes*). The gametes, therefore, are at the same time small spores ordinarily incapable of functioning as spores, and the transition from swimming spores to gametes, from the asexual to the sexual condition, seems clear. A cell that is indifferently a spore or a gamete, as shown by its behavior, can be recognized as one or the other, not from any fundamental difference in its structure, but only from its behavior. The origin of sex takes place, therefore, when a spore behaves as a gamete.

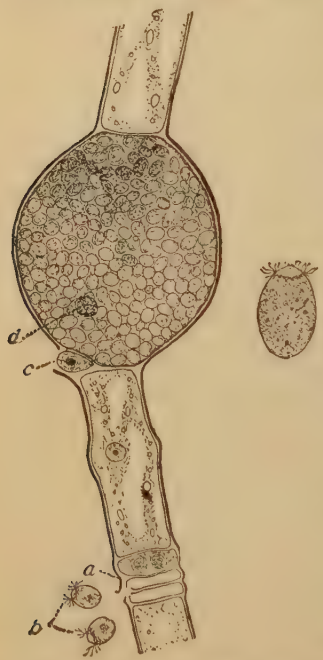

FIG. 6.—*Oedogonium*, showing discharged sperms (*b*) and spore (to the right of the filament), each with a crown of cilia; the large cell of the filament is the oögonium containing the egg, and the small cells (*a*) are antheridia from which sperms have escaped.

An incidental proof that gametes are derived from spores may be obtained from the variations in the swimming appendages of spores. Any peculiarity in these appendages is duplicated in the gametes. For example, in a certain green alga (*Oedogonium*) the spore is dis-

tinguished by bearing a crown of cilia, and the same crown appears in its motile gametes (Fig. 6). The spores of brown algae are peculiar in bearing two cilia laterally (instead of apically), and the same peculiarity occurs in the motile gametes (Fig. 7).

There is a difference in gamete-formation and spore-formation that remains to be described, for it is probably fundamental in connection with the origin of sex. In the illustration used, spores and gametes were represented as occurring simultaneously in the same individual, which would mean that they are produced under the same conditions. The fact is that usually they are not produced simultaneously by a plant. When the conditions favor vegetative activity, neither spores nor gametes are produced. When the conditions are less favorable for vegetative activity, spores are produced; and when the plant is approaching the end of its activity, gametes are produced. It is obvious that waning spore-production may sometimes overlap beginning

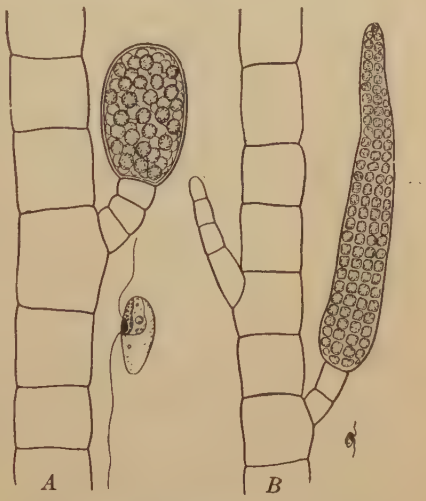

FIG. 7.—A brown alga (*Ectocarpus*): *A*, part of a filament showing a sporangium, and also an escaped spore; *B*, part of a filament showing a gametangium, and also an escaped gamete.

gamete-production, and so the two may appear together in a plant, but they are really differentiated by conditions, and usually distinctly separate in the time of appearance. It has been found possible to control experimentally among the algae the conditions that determine these various activities. The plant may be kept in vegetative activity indefinitely; it may be made to produce spores at any time; or it may be made to produce gametes. The distribution of these functions in the ordinary life history of the plant is naturally related to its changing environment. It begins the season with vegetative activity; later the conditions that favor luxuriant growth decline somewhat, and spore-formation begins. It is in this second period that the greatest multiplication of individuals occurs, so that although the plants are sexual, the chief amount of reproduction is by means of the asexual spores. In such algae as are being used as illustrations, the production of gametes is the last act in the life of the plant, an act induced by conditions that are bringing the activity of the plant to a close.

If the original difference between spores and gametes be considered, it seems evident that it depends upon the number of times the material of a protoplast is divided. If it is not divided at all, or only a few times, the cells produced are spores; if the divisions are more numerous, the cells produced are probably gametes. The conditions that favor gamete-formation rather than spore-formation, therefore, are conditions that favor successive divisions of the protoplast body before discharge. The divisions are regular cell divisions, which are soon checked in spore-formation but continue much longer

in gamete-formation. Why this cell division is favored in connection with the waning activity of a plant is not clear, but it seems to be a fact. The general conclusion may be reached that gametes appeared as a result of the aging of cells, which stimulates cell divisions in a spore-forming protoplast to such a degree that the resulting cells are incapable of functioning as spores.

This introduces a much more obscure problem. If spores become incapable of functioning on account of reduction in size, what induces them to pair and fuse? The two pairing gametes are evidently attracted to one another, as evidenced by their movements. They approach one another until they come in contact; and, moreover, their positions in reference to one another are definitely oriented, the ciliated ends touching one another. This is followed by a complete fusion of the two cells, apparently as complete as is the fusion of two globules of mercury. When the extremely complex structure of such cells is considered, their fusion is a process much more intricate than that of two globules of mercury. Whatever factors of heredity a spore contains are doubled in the cell produced by the fusion of gametes. This sexually formed cell, therefore, starts an individual with a very different equipment from that possessed by a spore; in fact, it may be called a double equipment. When one considers the mutual attraction of the two gametes, their definite orientation, their fusion, and the organization of a new cell from the fusion of two cells, it is impossible to escape the conclusion that, although gametes are obviously spores of reduced size, other more important differences have developed. The difference in size is visible, but in connection with

it there must have been developed a very different set of physiological conditions.

This first stage of gamete-production has been called *isogamy*, meaning that the pairing gametes are alike. Optically this is true, both of them resembling small motile spores that differ neither in size nor activity. The same idea is also expressed when such plants are said to be *unisexual*. Exception may be taken to both of these terms. The gametes are alike in appearance, but that they are not alike in fact is evidenced by their pairing and mutual attraction. Morphological likeness may justify the term isogamy, but there is certainly physiological unlikeness. The term unisexual has no excuse whatever. It means "one sex," which is impossible. Sexuality, with its pairing sexual cells, implies two sexes, whether they can be distinguished or not. All sexual plants must be bisexual to be sexual at all.

The original significance of sex, as indicated by the result of the sex act, remains to be considered. The cell formed by the fusion of two gametes is called a *zygote*. It has the powers of an ordinary spore in that it can produce a new individual, but the great difference in behavior is that it does not germinate immediately. It was produced under conditions unfavorable to vegetative activity, and therefore unfavorable for the production of a new individual. These unfavorable conditions, which favor the formation of a zygote, inhibit its activity, and it responds by developing a thick protective wall about the protoplast, and the protoplast itself passes into that inactive condition known as dormancy. In this protected condition, which is often wrongly called a resting condition, the

zygote passes through the unfavorable season, which is usually winter or a season of drought. In fact, the zygotes are usually the only representatives of the algae we have been considering, during the winter or during a drought period, all the vegetative bodies having disappeared. The original function of the zygote, therefore, is to carry a plant through from one growing season to the next. In other words, its most apparent significance is not so much reproduction as protection.

When favorable conditions for vegetative activity return, the zygote produces a new individual, and by means of spores individuals are multiplied during the growing season. Sexual reproduction in this case, therefore, although it results in the production of a new individual, does not multiply individuals. In fact, in many cases, even in the earliest of stages of sexual reproduction, the zygote does not produce an individual at all. When the revived protoplast resumes its activity, instead of functioning as a spore in germinating and producing a new individual, it divides at once to form spores, a swarm of spores escaping from the zygote (Fig. 8). In other words, the protoplast of a zygote, formed by the fusion of the gametes, that is, by the sex act, functions directly as a spore-producing protoplast. In such cases the only reproduction is by spores, sexual "reproduction" not reproducing, but only protecting a spore-forming protoplast.

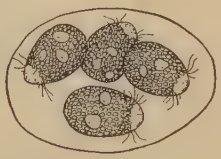

FIG. 8.—Four spores formed by the zygote of *Oedogonium*.

This variation in the behavior of the zygote of an alga when it becomes active is significant. In some

cases it produces spores, while in other cases it produces a vegetatively active individual. The inference is that the conditions for vegetative activity differ in the two cases. If the conditions favor maximum vegetative activity, a vegetative individual will be produced; but if they do not favor maximum vegetative activity, spores will be produced. That the second condition is the prevailing one is evidenced by the fact that in practically all of the heterogamous algae, and in many of the isogamous ones, the zygote produces spores. The situation is easily explained. The succession of conditions at the opening of a growing season is just the reverse of the succession at the ending of a growing season. In the latter case there is a gradually waning activity, resulting in spore-formation following vegetative activity; while at the opening of a season there is a gradually increasing activity, the conditions first favoring spore-formation and then vegetative activity. It is when early germinating conditions do not favor maximum vegetative activity that the protoplast of a zygote produces spores rather than a vegetative individual.

Although the relation of gametes to spores is made evident by such cases of overlapping functions as have been described, in most cases the two have become very distinct. In fact, gamete-production became separated from the ordinary activities of the body sooner than did spore-production, so that many plants with completely differentiated sex organs (*gametangia*) do not have distinct sporangia. The gametangia are produced under the same conditions that favor gamete-formation, so that the sex organs themselves are

responses to certain conditions, and are not inevitable structures. It is recognized that the so-called "fruiting period" of algae in general, by which is meant the appearance of sex organs and the formation of gametes, comes near the end of vegetative activity and closes the history of the plant for the season. It is not difficult to understand that a separation in time and in conditions, which would become more emphasized as life histories become more prolonged, would presently differentiate spores and gametes so completely that they would seem to hold no relation to one another.

This seasonal relation between spores and gametes should be emphasized, for it lies at the basis of the changes which gradually established a definite alternation of generations in the life histories of the higher plants. It should also be emphasized that spores are always as essential features of the life history as gametes, and that in plants, therefore, sexual reproduction is never the whole of reproduction. In fact, it is only among the highest plants that the zygote produces independent individuals. In the lower groups, the zygote practically only produces spores that do the real work of reproduction. Among the algae water is the medium in which the plant lives, so that the seasonal difference between spores and gametes could not be expected to result in much more than a protected zygote as the winter stage, and spores as the multipliers of individuals. When the land habit was attained, however, the resulting changes are striking, and the advance toward the condition of the higher plants is rapid.

A cytological situation must be indicated in this connection, which has an important bearing upon the

evolution of the life histories of plants. The nucleus of every living cell contains a definite number of chromosomes, bodies that are supposed to represent the physical basis of heredity, in the same sense that protoplasm represents the "physical basis of life." In other words, they are thought to be connected in some way with the reactions that transmit the characters of a parent to its progeny. The number of chromosomes is definite for each kind of plant and animal, and the characteristic number appears in every cell of the body. In different organisms the number ranges from two to more than a hundred. It is obvious that when two gametes fuse, the zygote contains the chromosomes of both; that is, the double number, as it is called. If the characteristic gamete number is 12, the zygote contains 24. Whenever the sex act (fertilization) occurs, therefore, the number of chromosomes is doubled. When the zygote produces a new individual, each cell of that individual contains the double number. Unless something should prevent, the chromosomes would continue to double with each succeeding generation, every time fertilization occurred, soon resulting in an impossible number. Sexual reproduction, therefore, necessarily involving a doubling of the chromosomes, must also involve a provision for reducing the number again. The life history of every sexual plant and animal, therefore, includes two principal events, namely, fertilization, which doubles the chromosomes, and some other process which reduces the number again.

The place of reduction in the life history varies, but in general among plants it occurs in connection with the formation of spores, which thus contain the half-

number; while among animals it occurs in connection with the formation of the sexual cells (gametes). The ordinary course of events among plants, therefore, is as follows. The zygote, containing the double number, produces a new individual, each of whose cells contains the double number. When this individual produces spores, the reduction occurs and the spores contain the half-number. The individuals produced by the spores in turn, of course contain the half-number, and when they produce gametes, fertilization doubles the number again. It is obvious that since gametes and spores both produce individuals, there must be two kinds of individuals, differing in the number of chromosomes. This difference, necessarily resulting from the fusion of gametes, lies at the basis of the subsequent evolution of plants. At the same time, it emphasizes further the large amount of change involved by the appearance of sexual reproduction. Among animals the situation is simpler, because reduction occurs in connection with gamete-formation, so that the gametes are the only cells with the reduced number of chromosomes, the zygote and all the body it produces having the double number. In this case there is no concurrent reproduction by spores to complicate the life history.

When spores and gametes are produced by the same individual, as is frequently the case among the lower plants, reduction generally occurs in the formation of gametes, in which case all individuals have the double number of chromosomes, as in animals. When it occurs in connection with the formation of spores, it is inevitable that the two kinds of individuals are produced. In a few plants, as in the common rockweed

(*Fucus*), the spores are eliminated, and, like animals, the reduction division is in connection with gamete-formation, and all the individuals are alike in the number of chromosomes. It should be emphasized again that two individuals are differentiated whenever reduction occurs in connection with spore-formation, for the difference in the number of chromosomes presently results in great differences in the appearance and functions of the two individuals.

The above statements in reference to the origin of sex may be summarized as follows:

(1) Gametes are derived from swimming spores which have become so reduced by successive divisions as to be incapable of functioning as spores.

(2) Gametes, when first recognized by their behavior, appear to be alike in every visible feature, so that there is no evident distinction of sex.

(3) A physiological differentiation of gametes is indicated by their mutual attraction in pairing, so that two sexes are present although not distinguishable.

(4) Gametes are formed under conditions relatively unfavorable to either vegetative activity or spore-formation, but favorable to successive cell divisions, and representing the closing activity of the plant.

(5) Gametes, therefore, appear in response to unfavorable conditions that arise in the life history of a plant that is long enough to extend through a considerable range of varying conditions.

(6) The sex act results in a zygote which is formed under conditions unfavorable to vegetative activity, and therefore passes into a protected, dormant condition, not germinating immediately as do the spores.

The conditions, therefore, which favor the formation of a zygote inhibit its germination.

(7) When a zygote becomes active, it may function like an ordinary spore, producing a new individual, or it may form spores, functioning like an ordinary spore-forming protoplast and not forming a new individual.

(8) The original significance of the sex act, therefore, is protection rather than reproduction, for its production of new individuals is negligible as compared with the number of individuals produced by spores.

(9) The physiological changes involved by the introduction of the sex act are very great and far reaching, for they include the mutual attraction of gametes (shown by pairing), the organization into a single cell of the contributions of two cells, a provision for reducing the number of chromosomes which the sexual fusion has doubled, and the appearance of two kinds of individuals produced by spores and zygotes.

CHAPTER III

THE DIFFERENTIATION OF SEX

The differentiation of sex to be discussed may be called in general morphological differentiation. In the preceding chapter attention was called to the fact that two pairing gametes, although alike in appearance, must be different physiologically. By morphological differentiation is meant difference in appearance, and therefore a visible difference. In the case of gametes, this visible difference involves size and activity, with such motile organs as may go with activity. In this sense, therefore, the differentiation of sex means such a differentiation of gametes that they can be recognized as male and female. Of course morphological differentiation must have been brought about by physiological differentiation, and the physiological changes, of which the morphological changes are but an index, must have been very great. Morphological likeness of pairing gametes, as stated in the preceding chapter, is called *isogamy*, while morphological unlikeness of pairing gametes is called *heterogamy*. In isogamous plants, therefore, the terms "male" and "female" are not used, but in heterogamous plants they become current.

The type of gamete that gradually gave rise to dissimilar gametes was clearly the active swimming-spore type, the two pairing gametes being alike in size and activity (Fig. 9). A series of algae can be arranged, beginning with gametes of this type, continuing step

by step through increasing differences in the pairing gametes, and ending with gametes so different in appearance that they do not suggest identical origin (Fig. 10). In fact, there are numerous cases in which it is doubtful whether the plants should be called isogamous or heterogamous, and any application of these differential terms seems arbitrary. This must not be regarded as the gradual differentiation of *maleness* and *femaleness*, but the gradual appearance of differences that make the two sexes recognizable.

FIG. 9. — The pairing and fusing of similar gametes and the resulting zygote of water-net (*Hydrodictyon*).

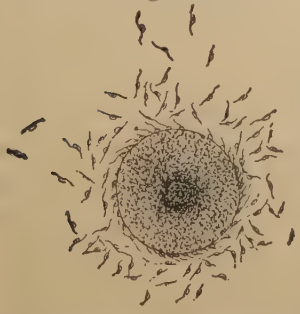

FIG. 10.—The large egg and small sperms of rockweed (*Fucus*).

In the series referred to, one of the pairing gametes becomes recognizably larger than the other, and this relative size gradually increases until finally it becomes many times greater than that of its mate (Fig. 10). This increase in the bulk of one of the pairing gametes is observed to be due chiefly to the increased bulk of cytoplasm, which is a region of the protoplast that seems to be concerned chiefly with the nutrition of the cell, whatever other activities it may carry on. For this reason, the larger gamete is said to have much greater nutritive capacity than its mate. Concurrently with increase in bulk there is gradual loss

of motility, the swimming appendages (cilia) finally disappearing, until the large gamete becomes a completely passive cell so far as motility is concerned. This relatively bulky gamete, with high nutritive capacity and no motility, is recognized as the female sexual cell, or *egg*. Whatever else happens when a small motile gamete is gradually transformed into an egg remains as yet in obscurity.

It is important to emphasize the fact that the increased size of an egg is due chiefly to the increased bulk of cytoplasm, and not to any greatly increased bulk of the nucleus. If the nucleus contains the physiological equipment for inheritance, in differentiating the egg this has not been sensibly increased, so that there is no reason to believe that the contribution of the egg to inheritance is any greater than that of its much smaller mate. On the other hand, if the cytoplasm contains the chief physiological equipment for nutrition, then the egg is much more concerned with the nutritive needs of the sexual process than is the other gamete. It is this relation to nutritive capacity that accounts for the fact that among heterogamous plants the production of eggs requires a better equipped nutritive body than the production of the other gametes. For example, among the ferns the small gametes may be produced abundantly by a very young or a very poorly developed body, but the eggs cannot be produced until the body is well developed.

The history of the other gamete in the series under consideration is quite different. There is no such increase in bulk; in fact there often seems to be a decrease. When this diminished size occurs, it is not

at the expense of the nucleus, but of the cytoplasm, so that in some cases the smaller gamete may be simply a nucleus ensheathed by a thin layer of cytoplasm. In the differentiation we are considering, therefore, it is the cytoplasm that is the variable in amount, while the nucleus is relatively constant. This emphasizes the common claim that the nucleus is the essential structure in the sexual act and in inheritance, while the cytoplasm is the source of the nutritive supply. The significant feature of the small gamete, however, is its motility, which it not only retains from its ancestral swimming spore, but also develops into greater efficiency. In fact, the smaller gametes differ in different groups of plants chiefly in the apparatus for locomotion, which is sometimes very elaborate. This relatively small gamete, with well-developed motility, is recognized as the male sexual cell, or *sperm*.

When one contrasts highly developed eggs and sperms, it is hard to imagine that they have been derived from the same type of cell and that cell a swimming spore, which is in turn an escaped protoplast, but numerous completely connected series of stages forbid any other conclusion. A few illustrations will indicate the ways in which this gradual differentiation of eggs and sperms may express itself, and will emphasize the essential features of the differentiation, for it will eliminate certain incidental features that have sometimes been regarded as of primary importance.

Among the brown algae there are forms in which swimming spores, undifferentiated gametes, and differentiated gametes are so closely associated in origin that they can be recognized only by behavior, and even then

it is not clear but that they might have behaved differently. In an organ which has been called both a sporangium and a gametangium, motile cells are produced which upon escape may either function as spores, germinating directly, or pair and fuse as gametes. When spores and gametes are produced by the same organ, the close relationship between the two seems obvious, but cases have been reported in which a gametangium (or sporangium) produces motile cells of three sizes. Those of medium size germinate directly as spores, while the largest and smallest ones pair and fuse as gametes. In this case not only are spores and gametes evidently related, but the gametes are somewhat differentiated in size, representing the beginnings of heterogamy. It has also been reported that the larger gamete, which is, of course, still motile, has been observed to come to rest before fertilization, and in this quiescent condition fuses with the small and persistently active gamete. In this case the gametes have begun to differ not only in size but also in motility.

In the cases just cited there seems to be evident a contradiction of a claim advanced in the preceding chapter, namely, that the zygote does not germinate immediately because it is formed under conditions unfavorable to vegetative activity, and therefore it becomes a protected and dormant cell. But among the brown algae just described, the spores germinate immediately, while the zygote formed at the same time, and apparently under the same conditions, always passes into the dormant and protected stage. There are two alternatives suggested as an answer. The conditions under which the spore germinates and under which the

zygote fails to germinate have not been analyzed, so that it is an assumption to claim that they are the same. The other alternative, however, introduces another factor that is probably a very real one in the delayed germination of zygotes. When the two sexual cells fuse, a new cell is organized, and this reorganization always involves more or less delay before the new cell is in a condition to divide. This fact has been observed repeatedly in the case of fertilized eggs (zygotes) which do not pass into a prolonged dormant period, and therefore are said in general to germinate at once. In other words, while unfavorable conditions for vegetative activity favor gamete-formation, and therefore zygote-formation, and at the same time tend to inhibit zygote-germination, the organization of a cell from the contributions of two cells also involves more or less delay in the expression of vegetative activity.

Spirogyra, a genus of green algae, exhibits some suggestive phenomena in connection with the differentiation of sex. The plants are simple filaments and produce no free-swimming spores or motile cells of any kind. What inhibits the escape of protoplasts as spores in this case is a problem. When the end of vegetative activity is approaching, the protoplasts separate from their walls and round off as if about to escape as spores. Instead of this, however, two filaments lying near together put out from each cell a tubular prolongation, which meets a similar one from the other filament. In this way a tubular passageway connects each cell of one filament with the adjacent cell of the other filament, and the two filaments thus connected resemble a ladder. Through these connecting tubes the

protoplasts of one filament pass into the cells of the other filament and fuse with their protoplasts, forming zygotes, which develop heavy walls and become dormant (Fig. 11).

There are several features of this performance that deserve attention. These protoplasts, which were the ordinary protoplasts of a vegetative body in conditions of vegetative activity, function as gametes without developing any special organization usually associated with gametes. It would seem, therefore, that any protoplast can function, not only as a spore, but also as a gamete, dependent upon the conditions. Moreover, although the two fusing protoplasts seem to be alike in every particular, they differ in behavior, for one remains quiescent, while its mate moves through the connecting tube. This differentiation of motility is a feature of egg and sperm, and, therefore, the two pairing protoplasts of *Spirogyra* may be regarded as distinctly male and female, although they do not differ in size. In this case there is a physiological differentiation which happens to make itself visible, and no morphological differentiation that is evident. Furthermore, often all of the protoplasts of a filament are either quiescent or motile, so that the filaments as a whole are male and female. This is a striking illustration of the fact that the same protoplast may function as a

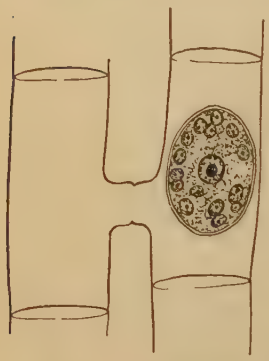

FIG. 11.—A zygote of *Spirogyra:* the connecting tube and empty male cell are also shown.

vegetative cell, a spore, a sperm, or an egg, determined by varying conditions; and, furthermore, that even a gamete does not necessarily differ in apparent structure from a vegetative protoplast.

Spirogyra furnishes a further illustration of the fact that conditions unfavorable to vegetative activity are at least partly responsible for the fact that a zygote becomes a dormant cell. When two filaments are being connected by conjugating tubes, as the connecting tubes are called, it sometimes happens that certain cells develop no connections with other cells. In this case the rounded-off protoplast has no opportunity to fuse with another one. Apparently it is a gamete without a chance to function, but it behaves as a spore. Instead of germinating promptly, as a spore usually does, it develops a thick wall and becomes dormant, just as a zygote, but it germinates promptly when the conditions become favorable. In other words, a spore behaves like a zygote when the conditions are the same. It is often stated that this protected and dormant spore is really a gamete that has not been fertilized, and therefore a case of parthenogenesis, but the difference between an unfertilized gamete that germinates and a spore would be hard to state.

Spirogyra is usually described as an isogamous plant because its gametes look alike and do not look like ordinary eggs and sperms, but they behave like eggs and sperms, and the individuals that produce them are often distinctly male and female. An interesting relative of *Spirogyra* has not differentiated its gametes in motility, and therefore is in a more primitive condition, so far as the sexual performance is concerned.

Both protoplasts (gametes) enter the conjugating tube, meet, and fuse, so that the zygotes are formed in the tubes and not in the cells. It is evident that the advance to the condition of *Spirogyra* is the entire loss of motility by one of the gametes and its retention by the other.

FIG. 12.—A red alga (*Nemalion*): at the left is the female sex organ; the figure at the right shows the result of fertilization.

Sexual reproduction among the red algae illustrates further the essential features of gametes. In this group there is a distinct differentiation of sex, so distinct that different male and female organs are present, well set apart from the vegetative body, but the sperms resemble ordinary protoplasts, not even detached from their walls. Sometimes they are discharged, but have no swimming appendages as true sperms ordinarily have, and sometimes they are not discharged. There is a distinct female organ (Fig. 12), usually of complex structure, but no egg that can be recognized as different from an ordinary protoplast. It does not even separate from its wall and round off, so that it is not called an egg. It is simply the protoplast of a cell that functions as a gamete, because the sperm or its nucleus enters and fuses with it. Among red algae, therefore, there is a very distinct

differentiation of sex, but there are no eggs and sperms in the ordinary sense, their rôle being played by two protoplasts not at all different in appearance from ordinary protoplasts. It must be evident that the essential feature of the sex act is the fusing of two protoplasts, and that all the observed modifications of these protoplasts as gametes of various appearance are secondary characters. Whether the nuclei alone are significant in this fusion in every case is a question that does not affect the general fact that the sex act is the fusion of two protoplasts which may be exceedingly variable in appearance and behavior. There is no apparent reason why any two protoplasts under appropriate conditions may not function as gametes. There can be no question but that the differentiation represented by well-developed eggs and sperms facilitates the sex act and makes it more effective, but it is not the essential feature of it.

Among the heterogamous plants the variable gamete in appearance is the sperm, and its variability has to do chiefly with its swimming appendages, its form, and its amount of cytoplasm. Some illustrations of these variations will help to an understanding of the real character of a sperm, as shown by the features that all sperms have in common.

Among the algae the sperms usually resemble closely the swimming spores of the same plant except in size. If the spores are terminally biciliated or laterally biciliated, with a crown of cilia or with no cilia at all, the sperms show the same features. In these cases it seems evident that sperms have not become specialized in the mechanism for locomotion.

The stoneworts (Charales) are often included among the green algae, but with no very good reason. In any event, their sperms are more highly specialized than those of any thallophytes. The ensheathing cytoplasm is extended into a long and more or less spirally coiled beak which bears at its tip two long cilia (Fig. 13). Such a sperm, therefore, is differentiated into two regions, namely, the *body* (containing the nucleus) and the *beak* (bearing the swimming appendages). That this more elaborate structure is concerned with greater efficiency in locomotion, and not with any change in the essential function of the sperm, seems evident, and yet a beak is often spoken of as essential to a sperm, although there are too many sperms without beaks to make this statement admissible.

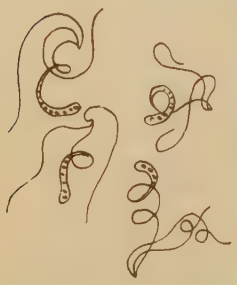

FIG. 13.—Sperms of a stonewort (*Chara*).

Among the bryophytes (liverworts and mosses) the sperm is relatively simple, consisting of a small, sometimes curved body, a more or less evident beak, and two long cilia (Fig. 14). It is but little more specialized than an ordinary swimming spore with two terminal cilia, and this same relative simplicity is continued among the club mosses. In these groups the general resemblances to the spores of the same plant have disappeared, for the spores have become aerial structures, no longer equipped for swimming. It is a noteworthy fact, to be discussed more fully later, that when the land habit was established

FIG. 14. —Sperm of a liverwort.

among plants, spores responded promptly to the aerial conditions, but sperms long persisted as swimming cells.

Among the ferns and gymnosperms, however, the sperm reaches its most extreme specialization in the apparatus for locomotion. Among ferns the body is unusually large for a sperm, and is spirally coiled, while a conspicuous cytoplasmic beak bears numerous (40 to 50) long, retrorse cilia (Fig. 15). Among the primitive gymnosperm groups there is the same large body, but instead of a cilia-bearing beak, the numerous cilia are developed in a spiral band about the body, which thus appears superficially as if spirally coiled (Fig. 16). In connection with the development of such an elaborate ciliary mechanism, a special organ of the cell (*blepharoplast*) has appeared, which functions during the organization of sperms as a cilia-former.

FIG. 15.—Sperm of a fern.

FIG. 16.—Sperm of a cycad.

Among the angiosperms (flowering plants) and more modern gymnosperms, however, a very different situation has developed. Instead of the sperms of these groups showing still further specialization in the organization of the apparatus for locomotion, motility itself has disappeared, even in its simplest expression (Fig. 17). This disappearance of motility as a feature of sperms is associated with the development of another method by which the sperm approaches the egg. The so-called "pollen tube," as it advances in growth from the male organ to the egg, carries the passive sperms. In the

highest plant groups, therefore, the sperm is no longer a swimming cell, needing a liquid medium to secure approach to the egg, but is as passive as the egg itself. The significant feature of this change is that it indicates clearly that all the elaborate specialization of the sperms of ferns and gymnosperms has to do with their motility, and not at all with their function as gametes. It shows further that even the simple cilia of the original gametes are no essential part of a sexual cell, any more than oars are essential to human beings. The need for emphasizing this is apparent when it is known that this secondary feature of a sperm was regarded formerly as its essential feature by those who demand rigid categories. For this reason, when motile sperms were first discovered in gymnosperms, they were hailed by many as the only sperms in seed plants. In other words, the sperms of most seed plants were not regarded as sperms because they could not swim.

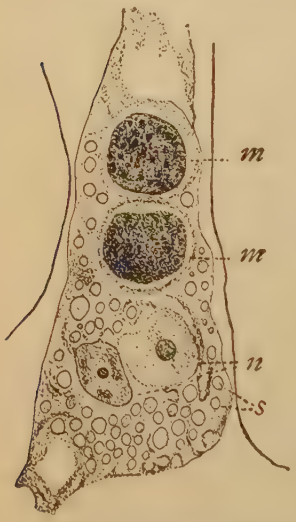

FIG. 17.—Sperms (*m*) of pine, in tip of pollen tube.

Another feature of the sperms of angiosperms deserves to be mentioned. The ciliated sperms of the other groups are produced by "mother-cells," within which they are formed and from which they are discharged, so that in spermatogenesis mother-cell and sperm belong to different cell generations. This morphological fact

led to so rigid a definition of a sperm that if the sperm generation was omitted it was concluded that there were no sperms. For example, this is just what happens in the spermatogenesis of all angiosperms and many gymnosperms. The cell generations succeed one another until the mother-cell appears, but it does not organize and discharge a sperm. The usual formula for describing this situation has been to say that "the mother-cell functions directly as a sperm," implying that in fact there is no sperm, but that the mother-cell behaves like one. Since the test of a gamete through all its history has been its behavior, it is difficult to understand such a statement except that a secondary feature has been substituted for the essential one. Moreover, the situation is explained easily on the basis of what has been observed in connection with spore-formation. Under certain conditions, it will be remembered, protoplasts separate from their walls and are discharged as spores, thus securing the opportunity to produce new individuals rather than to contribute merely to the growth of a single individual. In the same way protoplasts separate from their walls and are discharged as swimming sperms. It is obvious that if organization by a mother-cell and discharge of a sperm are essential to secure freedom of approach to the egg, when another method of approach is secured the necessity for discharge will disappear. The protoplast within the mother-cell and the discharged sperm are the same protoplast, and the mother-cell of angiosperms behaves like a sperm, therefore, because it is a sperm; one without swimming apparatus or organization of any kind that differs in appearance from the protoplast of an ordinary cell.

The conclusion, therefore, is that a sperm is a protoplast that fuses with another one to form a zygote; that in visible features it differs in no essential way from any other protoplast; that eventually it becomes much less bulky than its mate on account of a difference in the amount of cytoplasm; that it often develops an elaborate swimming mechanism as a secondary feature; and that the swimming apparatus is suppressed when the necessity for swimming disappears.

The statement that sperms persistently retain the swimming habit long after plants in general acquired the land habit deserves further consideration. It is obvious that in land plants whose sexual reproduction demands water as a condition for fertilization, this act would take place only occasionally, when the conditions happened to favor it. Spores could be formed freely and scattered, so that spore-germination could proceed in the ordinary conditions of plant growth. It is true that many land plants grow in conditions of moisture sufficient to permit fertilization, but many do not. For example, many mosses grow in exceedingly dry habitats, where conditions for fertilization very rarely occur. In fact, in not a few mosses sexual reproduction is rare, and in some of them it has not been found to occur. Apparently as a compensation, mosses have a remarkable power of vegetative multiplication, a single individual thus being able to produce a "bed of moss." It is common observation that mosses occur in masses, and this is not due to active sexual reproduction, but to vegetative multiplication. This further emphasizes the fact that after sexual reproduction had appeared and had been highly developed, it often failed to be

concerned in the major part of reproduction. In many land plants fertilization is only an occasional process, a fact explained chiefly by its persistent need for conditions that permit sperms to swim. It is inconceivable that if the sex act were essential to reproduction the sperms would not have responded to aerial conditions as promptly as the spores. How the appropriate conditions for sperms have been secured by various groups of land plants with varying degrees of success will be considered in a later chapter.

One of the interesting problems connected with sperms is their attraction and therefore movement, not only toward eggs, but also toward the appropriate eggs. For example, if the female sex organs of mosses and ferns be intermixed in a culture and fern sperms be supplied, they will seek out the eggs of ferns, not approaching those of mosses, and vice versa. It is obvious in this case that the eggs of ferns have a specific attraction for the sperms of ferns, which the eggs of mosses do not possess. In these forms the sperms can be experimented with so easily that it was discovered that the fern sperm responds to one organic acid and the moss sperm to another acid, the specific acid in each case being supplied by the egg or closely adjacent cells. If the specific acid is supplied, the corresponding sperm moves toward it, whether it is associated with an egg or not. This kind of response is called *chemotaxy*, which simply means a response to a specific chemical substance. This is the statement of a fact rather than an explanation, but it suggests that pairing of gametes may be in response to what may be called chemical attraction. When this attraction exists and both

gametes are free to move, they move toward each other; and if one is non-motile, its mate shows all the activity. Such mutual attraction means a physiological difference, so that this distinction of sex is present even in isogamous plants. It is the development of this difference in passing from swimming spores to gametes that makes the latter function as sexual cells; and when this physiological difference which results in mutual attraction is discovered, the real origin of sex will have been discovered.

When neither sperm nor egg are motile, as is true of all angiosperms and many gymnosperms, the existence of this same mutual attraction is evident by the fact that when they are brought near together by some substitute for motility they come in contact, become closely pressed together, and finally fuse. For example, in angiosperms the sperms are carried by the pollen tube to the egg cavity and discharged into it in proximity to the egg, but at this point the sperm approaches the egg and fuses with it. What may be called the "sphere of attraction" may vary widely in extent in different cases, but the existence of such an attraction seems evident in all cases of pairing and fusing.

A peculiar phenomenon connected with fertilization occurs in angiosperms which makes the fusion of sperm and egg seem less like a phenomenon peculiar to them. Two sperms are discharged into the egg cavity. One of them moves to the solitary egg and fuses with it. The other sperm moves toward another cell in the egg cavity and fuses with it, as though it were another egg. That this second cell is not an egg is shown by the result. The true egg when fertilized begins the development of a new individual (the embryo), while the other cell, after fusion with the second sperm, does not produce

a new individual, but develops the nutritive tissue called *endosperm*, and yet between it and the sperm there was the same mutual attraction as between the egg and sperm, leading to contact and fusion. This would indicate that the mutual attraction and fusion of two protoplasts is not all that is necessary for the production of a new individual, and that mutual attraction is as much a secondary feature of sex reproduction as is motility, and simply directs motility. In such plants, therefore, there must be some fundamental difference between an ordinary cell and one that has matured as an egg, but at the same time probably any protoplast may mature as an egg.

It is among angiosperms also that the clearest evidence has been obtained that the essential fusion in the act of fertilization is the fusion of nuclei, and that fusing cytoplasm plays a subordinate rôle, which may be omitted entirely. In most angiosperms the cytoplasm investing the nucleus of the sperm is a very thin layer, so that its significance in fertilization has long been questioned; but in certain angiosperms it was discovered finally that when a sperm is discharged from the pollen tube the nucleus slips out of its cytoplasmic sheath and enters the egg cavity as a naked nucleus, the empty sheath remaining in the pollen tube. Whatever significance, therefore, there is in the sex act is found in the fusion of nuclei, and the cytoplasm is a secondary feature, just as motile organs and mutual attraction.

When two protoplasts fuse, therefore, and do not produce a new individual, their nuclei must differ in some way from those of functioning sperms and eggs. That this difference has to do with the constitution of the cell organized after the fusion seems evident, for

many cells without fusion produce new individuals. One may imagine the adjustment of one nucleus to another before fusion can result in reproduction, and this mutual adjustment probably lies at the basis of sexual reproduction. It also probably explains the fact that sperms and eggs vary in their ability to fuse and in the results of fusion. A certain amount of affinity (relationship in origin) is necessary between a sperm and egg, much more restricted in some cases than in others, if the sexual act occurs or if it results in reproduction. Even when the affinity seems to be close enough, still the result may be sterility. It often happens in angiosperms that not only does the fertilized egg produce an embryo (a new individual), but any cell in the egg cavity or any of the cells surrounding the egg cavity may produce an embryo. This is the phenomenon called *polyembryony*, and as many as five embryos have been observed in a single egg cavity. Of these five embryos, one was produced by the fertilized egg and four by cells without fusion, some of them clearly ordinary vegetative cells. In some cases the fertilized egg fails to reproduce, or the sperm and egg are unable to fuse, but the neighboring cells produce embryos. It seems evident that successful fusion and reproduction involve an adjustment of one nucleus to the other; an adjustment which is not required for reproduction in unfused protoplasts. This mutual adjustment of two nuclei, so that they can fuse and organize a new cell capable of reproduction, is the mechanism of sex, a mechanism that is more easily interfered with than any other mechanism of reproduction.

Even if the *mechanism* of sex is of the general nature suggested above, it must not be confused with the

significance of sex. That sex is not necessary for reproduction is clear, and that it never results in as many individuals among plants as do the asexual methods of reproduction is also clear. Its significance, therefore, must lie in the fact that it secures something in connection with reproduction which the other methods do not, at least to so great a degree. It seems most rational to conclude that this significance lies in the fact that the sexual method of reproduction multiplies variation as no other method of reproduction can. When two cells, often of different ancestry, inheriting characters from two independent lines, unite to form a new cell, there is a combination of characters for selection that no other method of reproduction can secure. It is not strange, therefore, that no two individuals among the progeny from sexual reproduction are alike. Sex reproduction, therefore, secures extreme individuality, and it is individual variation that makes evolutionary processes possible. The cell fusion preceding the reproduction of a new individual is not necessary to reproduction, therefore, but it is necessary to make the individual produced differ from every other individual. The extensive and varied evolution of the plant kingdom, therefore, seems to have arisen from the abundance of variable material furnished by sexual reproduction. This is far from meaning that there is no variation apart from sexual reproduction; numerous facts would contradict such a claim; but it does mean that variation is enormously multiplied by sexual reproduction, and that therefore the progress of plants and their great diversity has depended more upon sexual reproduction than upon any other cause.

CHAPTER IV

THE EVOLUTION OF SEX ORGANS

When gametes first appeared among the algae as modified swimming spores, they were produced by the protoplasts of ordinary vegetative cells, which under different conditions functioned vegetatively, divided to form spores, or divided to form gametes. The first differentiation was the production of special gamete-producing cells (*gametangia*). This seems to have preceded the differentiation of spore-producing cells (*sporangia*), and the reason appears obvious. The conditions favoring gamete-production are much more differentiated from those favoring vegetative activity than are those favoring spore-formation. The production of gametes belongs to the end of seasonal activity, and thus the function of the cells producing them is distinctly set apart in time from the function of ordinary cells.

In many cases ordinary vegetative cells, functioning later in the season as gametangia, become transformed in appearance, so that they are as different in appearance from ordinary cells as they are in function (Fig. 18). This may be regarded as an intermediate stage between gametangia which are unchanged vegetative cells, and those which are never vegetative cells. The three stages in the differentiation of a sex organ, therefore, are: (1) a vegetative cell changed in function; (2) a vegetative cell changed in form as well as in function; (3) a cell which is never a vegetative cell.

The gamete-producing cells finally come to be produced later than the others, their formation being induced by the same conditions that favor gamete-formation. As has been said, gametangia are not formed along with the ordinary body cells, to await suitable conditions for functioning. If this were true, they probably never would become distinct from ordinary cells. They were produced under different conditions, and therefore were differentiated from the rest of the body. In other words, the conditions that made gametes differ from other protoplasts subsequently made the gamete-producing cells differ from ordinary cells.

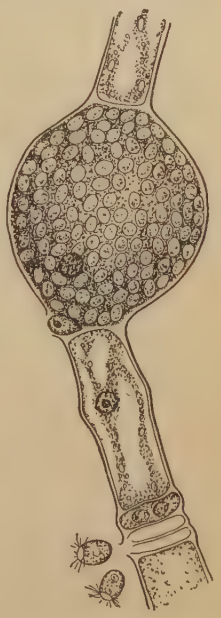

FIG. 18.—Sex organs of *Oedogonium:* the large cell (oögonium) contains the egg; the two small cells (antheridia) have just discharged sperms.

When gametes were differentiated into eggs and sperms, it was inevitable that the gametangia should become differentiated also. The relatively large and passive eggs would determine the form of a gametangium quite different from that producing the small and active sperms. At the first appearance of these distinct male and female organs among the algae, they are cells appearing usually as late appendages upon the body of the plant (Fig. 19). The female organ (*oögonium*) is naturally the more conspicuous one, becoming a relatively large spherical cell,

which usually produces a single egg; while the male organ (*antheridium*) is a relatively inconspicuous cell which produces a variable number of sperms. Throughout the algae, with their water environment, the sex organs retain this simple character.

An interesting situation is developed by the sex organs of stoneworts (Charales). This group is usually included among the thallophytes, but has always suggested that it deserves a much higher position on account of its vegetative body and also because of its sex organs. The sex organs are much more complex than those of any other thallophytes, and the antheridium is the most complex sex organ known among plants. The greater complexity of the sex organs of liverworts and mosses as compared with those of algae has been explained as due to the difference in habitats, the liverworts for the most part being land plants, or at least exposed to the air, while the algae are water plants. The greater complexity of the sex organs of liverworts, therefore, could be explained as a protective response to air exposure. The Charales, however, are submerged water plants, forming mossy patches on the muddy bottom of ponds and still waters, and yet the sex organs, at least the antheridia, are more complex than those of the liverworts. It is a different kind of complexity, however, as will be shown later, and the complexity of the sex organs of liverworts is still best explained as a response to aerial conditions.

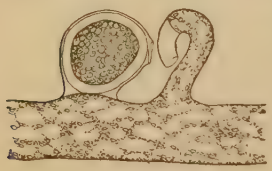

FIG. 19.—Oögonium and antheridium of an alga (*Vaucheria*) appearing as appendages on the vegetative body.

What may have been the origin of the complexities of the sex organs of Charales is left entirely to the imagination, since the group seems to be unrelated to any existing group. That its history has passed through conditions that demanded protection is witnessed by many of its vegetative bodies as well as by its sex organs. In such a case, the two alternatives suggested as to the possible conditions in which the ancestral forms lived are that they were either aerial conditions or marine conditions (including brackish water). In any event, while the sex organs of Charales are complex, the nature of the complexity does not suggest that of existing aerial or marine plants. Such detached groups are met with in every general region of the plant kingdom, and their detachment from other groups means that no evidence is available that indicates their historical connections. Doubtless if these connections of Charales were known as well as those of liverworts, there could be obtained suggestions as to the origin of their sex organs. None the less, it is interesting to observe the kind of complexities attained by this group.

The egg-forming cell is an oögonium like that of ordinary algae, but from a cell beneath a number of filaments arise that twine in a spiral about the oögonium and completely invest it, later forming a hard case (Fig. 20). Such an investment might suggest exposure to air, but it may as well mean exposure to conditions unfavorable to vegetative activity. In other words, after fertilization this case of cells holds the same physiological relation to the fertilized egg as does the thickened wall of the zygote of ordinary algae. This would mean that the protective response which usually follows

fertilization may involve the wall of the fertilized egg itself, or it may involve cells investing the egg. Among the Charales, therefore, the conditions that favor oögonium-formation favor also the development of cells investing the oögonium, and these cells form the protective structure induced by conditions unfavorable

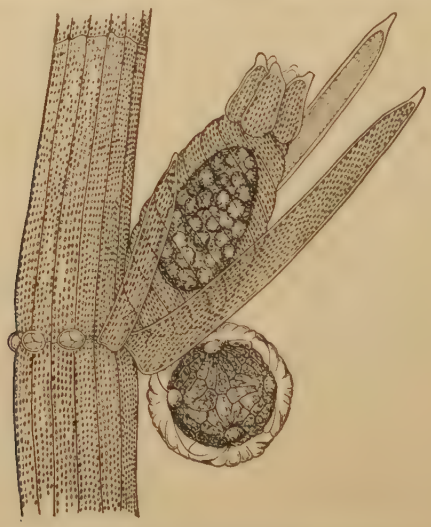

FIG. 20.—Oögonium (above) and antheridium (below) of *Chara*.

to germination. Fertilized eggs, therefore, cease to develop heavy walls, that is, cease to become what are often spoken of as "resting cells," when a tissue of investing cells responds to the unfavorable conditions. The total structure, including the egg-producing cell and its investing cells, is called the oögonium, the female sex organ, but it is obvious that the investing cells are secondary features of the organ, and that the central feature, as always, is the egg-producing cell.

While the oögonium of Charales might be related to the known female organs of other groups, no such statement can be made concerning the antheridium. After seeing the oögonium, one might expect the antheridium to be a sperm-producing cell, such as it is among the ordinary algae, invested by protective cells, but the situation is far more complex. Heavy-walled and interlocking cells form a spherical case, and within the case, in fact, arising from the incasing cells, is an elaborate succession of cells that finally ends in numerous delicate filaments, so that the antheridium seems to be a globular case packed full with a tangle of threads (Fig. 21). Each thread consists approximately of 200 cells, and each cell produces a sperm, so that the sperm output of such an antheridium may reach as high as 50,000. The highly specialized character of these sperms was referred to in the preceding chapter, as shown by the spirally coiled body and the elongated cytoplasmic beak tipped with two long cilia. It would be as useless to speculate as to how such a highly complex structure as this antheridium originated, as it would be to imagine the evolution of a seed if only seed plants existed.

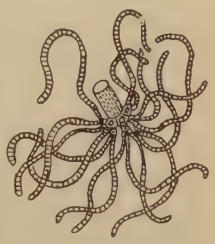

FIG. 21.—Filaments within antheridium of *Chara*, each of whose cells produces a sperm.

An interesting counterpart of this situation among the Charales is shown by the sex organs of the red algae. In this group, mostly marine, the female sex organ is often very complex, while the male sex organ is so simple that it suggests a reduced structure. The complexity

of the female organ does not involve the egg-producing cell itself, but consists in the number of secondary cells associated with it in function. In fact, the female sexual cell does not produce an egg morphologically distinct from the original protoplast of the cell. This original protoplast remains unchanged in appearance,

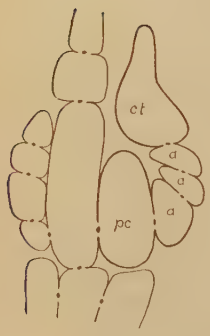

FIG. 22

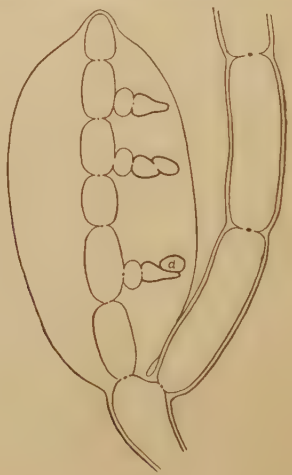

FIG. 23

FIGS. 22, 23.—Sex organ of a red alga (*Polysiphonia*): Fig. 22, the female organ (procarp); Fig. 23, the cluster of forming antheridia (*a*).

but its physiological differentiation is indicated when its nucleus fuses with the sperm nucleus. This is often spoken of as fertilizing a cell rather than an egg, but such a distinction is morphological; physiologically, the protoplast which rounds up as an egg and the one which does not, but is fertilized, are the same. However, morphology has refused to call this eggless cell an oögonium, naming it a *carpogonium*, but this carpogonium has associated with it a variable number of cells, all of

which, taken together, form the female organ, called in this group a *procarp* (Fig. 22). The constantly associated cell is one that catches the sperm and provides for it a passageway to the carpogonium. Since this receiving-cell often resembles a hairlike extension of the carpogonium, it has been named the *trichogyne*. The other associated cells which appear in most red algae are concerned chiefly with processes that follow the act of fertilization, and result in a spore-producing structure whose place in the life history of the red algae will be discussed later. These associated cells are well named *auxiliary cells*. The secondary cells, therefore, which make the female sex organ (procarp) of the red algae a complex structure, are not protective cells as in the Charales, but are associated actively with the essential cell in the act of fertilization and its results.

The antheridium, on the other hand, has no associated cells, but is a single small cell which does not form motile sperms (Fig. 23). In some cases it discharges its protoplast, which is said "to function as a sperm." This again represents a morphological point of view, because if it functions as a sperm it is a sperm. This illustrates further how secondary characters can often be made to replace the primary one. In this case, the discharged protoplast which "functions as a sperm" was not regarded as the true sperm because it was non-motile, and so it was called a *spermatium*, meaning that it is sperm-like in function but not in cilia, and therefore not a real sperm. In some cases this non-ciliated sperm is not even discharged from its antheridium, but the antheridium breaks off from the parent plant and is floated to the trichogyne, into which its protoplast

enters. This floating antheridium was also called a spermatium. In fact, it is the same protoplast, whether ciliated, discharged, or retained, and in every case it is a sperm because of its function.

The sex organs of the Charales and the red algae must be regarded as organs developed under peculiar conditions which led to peculiar results, but in both cases the sequence of changes leading to these results has left no evidence that enables us to reconstruct it.

The condition of sex organs among the fungi is of great interest, for in general this assemblage of forms may be regarded as having been derived from the algae, and it introduces very different conditions of living. It is possible, therefore, to observe what seems to be the effect of the dependent habit upon the development of the sex organs.

In one of the three great groups of fungi, much the smallest one, the ordinary sexual organs of the algae are present, and for this reason the group is named Phycomycetes ("algal fungi"). Oögonia and antheridia may be recognized as having the same method of origin and structure they show among the algae. Two features, however, deserve a passing notice. These fungi obtain their food either as parasites upon living plants and animals, or as saprophytes upon organic material that is no longer associated with a living body. This relates their vegetative activity very definitely to the food supply. When this supply begins to fail, and vegetative activity declines, the sex organs are produced and fertilization occurs. As a consequence, the zygote of necessity passes into the dormant stage. This emphasizes, with great definiteness, the relation

of the appearance of sex organs and the act of fertilization to declining vegetative activity, a relation which has resulted in a differentiation of sex organs from the rest of the body.

The other feature deserving remark is a substitute for the motility of sperms. The use of plants or animals as hosts seems to preclude the use of motile sperms. Certainly the regular appearance of conditions

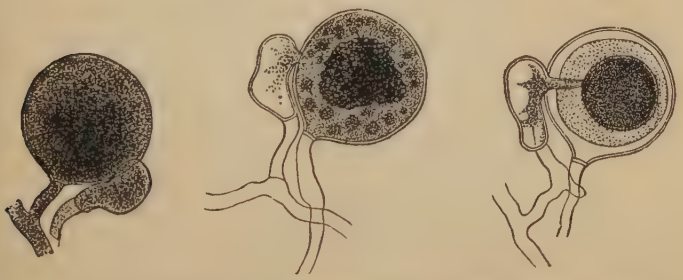

FIG. 24.—Oögonia and antheridia of a fungus (downy mildew), showing the antheridial tube.

for swimming would disappear. In general, therefore, antheridia and oögonia develop in proximity to one another, often coming into actual contact. The effect of the proximity or contact of an oögonium upon the behavior of an antheridium is noteworthy. As a response to the mutual attraction always exhibited by two pairing gametes, the antheridium develops a tubular extension which penetrates the oögonium and discharges the nuclei-containing protoplast of the antheridium into the protoplast or egg of the oögonium (Fig. 24). This growth-response of the antheridium seems to belong to the same category as the direction-response of swimming sperms. Direction of growth or

direction of movement, therefore, would be responses to the same physiological situation, the selection of one or the other form of response being determined by the condition of the structures.

It is in the other and much larger group of fungi, however, that the possible effect of the dependent habit upon the development of sex organs is shown. In general, the tendency is to eliminate the sex organs as structures distinct from the rest of the body. This must not be understood as the elimination of the sex act. This caution is necessary because the statement is often made that the dependent habit is a "blow at sexuality." Sex organs and sexuality are very different things. There was sexuality long before there were sex organs, so that sex organs may disappear and sexuality remain. In the larger one of the two groups of fungi under consideration, known as Ascomycetes, sex organs have been found in all stages of distinctness, from a condition in which they are as sharply differentiated as are the sex organs of ordinary algae, to one in which they resemble the ordinary cells of the body so closely that there is hardly any morphological differentiation at all. In a group so large, and one in which complete life histories are so difficult to obtain, it is unsafe to generalize too confidently as to the condition of the sex organs, but the life histories that are known indicate that sex organs occur in all stages of disappearance, and that in most forms they have disappeared entirely in the sense of being morphologically different from the ordinary cells of the body. In other words, the sequence leading to the differentiation of distinct sex organs, as shown by the ordinary algae, is reversed

among these fungi, leading to a morphological merging again of distinct sex organs with ordinary cells. It is a reversed evolutionary process, and that it is connected in some way with the dependent habit is further evidenced by the fact that the same thing has happened in the flowering plants (angiosperms) in connection with an extremely dependent habit. This condition among angiosperms will be described more fully later, but it is mentioned in this connection to emphasize the association of the disappearance of sex organs with the dependent habit.

Whether the sex act is eliminated from the life history of any ascomycete or not is an open question, for since it may merely involve a nuclear fusion, and nuclear fusions occur which are not sexual, a sex act may long escape observation, or may not be recognized with certainty when seen. For example, in the life histories of some Ascomycetes two different nuclear fusions occur, both of which cannot be sex acts, and one of them probably is. In any event, the tendency among these fungi has been to reduce the sex act to its essential feature, and in a reduction series it is entirely possible that the reduction in some cases may have reached a stage preceding sexuality.

In the other large group of fungi under consideration, known as the Basidiomycetes, and to which such well-known forms as rusts and mushrooms belong, the elimination of sex organs seems to be complete. As a consequence, even the presence of sexuality among the Basidiomycetes has been questioned. In any event, in a portion of their life histories two nuclei are observed consorting in the cells generation after generation, but

without fusing. Finally, at some period in the life history their fusion occurs, and this is followed by cell generations which are uninucleate. If this fusion represents the sex act, the gametic nuclei are long in proximity before they develop the mutual attraction that leads to contact and fusion. It might be regarded as the last stage before the complete elimination of sex.

The special features of the sex organs of Charales and red algae, and the apparent reduction of sex organs among fungi, do not represent the general evolution of sex organs. They are special lines of evolution in response to special conditions. The general line of evolution proceeded from the simple oögonia and antheridia of the ordinary algae to the sex organs of liverworts, which may be regarded as representing the second stage in the general evolution of sex organs. The conditions that determine this transition must be considered.

It is generally conceded that the transition from the green algae to the liverworts was associated with the acquisition of the land habit by plants. The algae are essentially water plants, and all their structures and habits are to be explained by that fact. As certain of the green algae acquired the ability to endure aerial conditions, they became so changed in structure that they constituted the most primitive land group, the liverworts. The appearance of liverworts was one of the most important epochs in the history of plants, for it was the beginning of a land flora, which led on to the higher groups of plants. The total structure of a simple liverwort can be explained as a response to aerial con-

ditions. Exposure to air means constant danger of excessive loss of moisture, which is fatal to living cells. Algae are not exposed to this danger, and to meet it liverworts needed to develop a structure that would

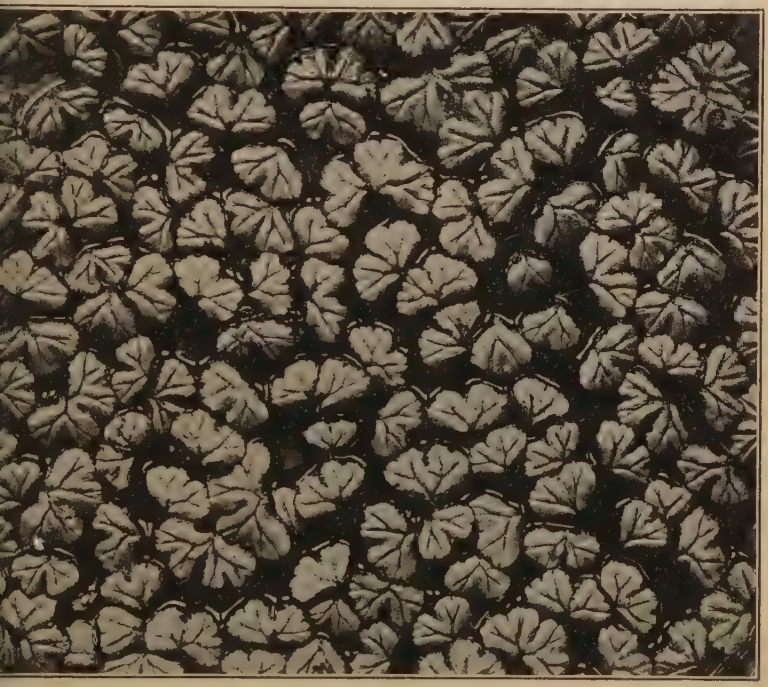

FIG. 25.—A group of floating liverworts (*Riccia*).

protect them. A compact body was the first desideratum, which would reduce to a minimum the exposure of cells to the air. This simply means that only algae with compact bodies could have made a start toward acquiring the land habit. Next, the prostrate position upon a moist surface would mean the minimum exposure

of the plant body. Finally, gradual exposure led to that modification of the superficial cells which resulted in a distinct epidermal layer, which forms a waterproof jacket about the bodies of all plants exposed to the air. The epidermis is a waterproof jacket whose efficiency lies in preventing the escape of water rather than in preventing its entrance. A compact, prostrate body, covered by an epidermis, is well equipped to endure exposure to the air (Fig. 25).

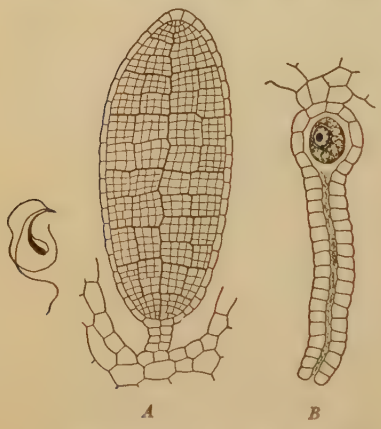

FIG. 26.—Sex organs of a liverwort (*Marchantia*): *A*, antheridium and a sperm; *B*, archegonium containing the egg.

The sex organs are developed upon the upper surface of the prostrate body, and are exposed to the same danger of desiccation as are cells of the working body. Accordingly they have become jacketed also (Fig. 26). In other words, the second general stage in the evolution of sex organs, which seems to be a much more complex stage, appears so only on account of secondary structures developed in response to exposure to air. An oögonium and an antheridium of an alga, each invested by a protecting jacket of cells, would represent the essential idea of the sex organs of liverworts. The male sex organ continues to be called an antheridium, but the female organ is now called an *archegonium*, a name which

belongs to the female sex organs of all groups above the thallophytes.

When one examines the antheridia and archegonia of liverworts, it seems evident that they did not arise from the simpler gametangia of algae, which are only single cells. At least there are other kinds of gametangia among the algae that represent what would be a more probable type for transformation into the antheridia and archegonia of liverworts. The type referred to is not common among the living algae, but it is certainly a gametangium with a structure that might easily be transformed into the jacketed sex organs of liverworts. It is best represented in some of the brown algae, and consists of a many-celled structure, each cell producing a gamete (Fig. 27). In short, it is like a mass of one-celled antheridia or oögonia. It is this type that has been used in explaining the origin of the antheridia and archegonia of liverworts and the higher plants.

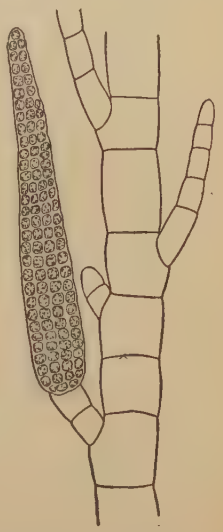

FIG. 27.—Gametangium of a brown alga (*Ectocarpus*).

The antheridium of liverworts is just such a mass of cells, with its superficial layer sterilized (not producing sperms) and forming a protective jacket. Since the superficial working cells of the body have been transformed by exposure into an inactive and protective epidermal layer, it seems altogether reasonable to suppose that the same thing might happen to such a

gametangium as referred to, and this would result in just such a structure as the antheridium of higher plants.

The archegonium is not so easily explained. A mature archegonium is in general a flask-shaped organ containing a single egg in the bottom of the flask. The flask is formed by the sterile jacket, and is differentiated into a *neck* and a more or less enlarged *venter*, the latter containing the egg, and the former constituting a more or less elongated passageway to it. The mature archegonium hardly suggests any possible connection with such a multicellular gametangium as we have been considering, but the developing archegonium is very suggestive (Fig. 28). The archegonium develops as an axial row of cells invested by a jacket of cells. Each cell of this axial row is probably a potential egg-producing cell, but usually only the lowest one matures as an egg, and this fact explains the enlarged venter. The other cells of the axial row become disorganized and thus open a passageway from the tip of the neck to the egg. The disorganization of this region of the axial row explains the comparatively slender neck. If our multicellular gametangium had narrowed enough to consist of a single row of egg-producing cells after the superficial row of cells had become sterilized, the result would be an archegonium. This connection is further suggested by the occasional appearance in a developing archegonium of two rows of axial cells,

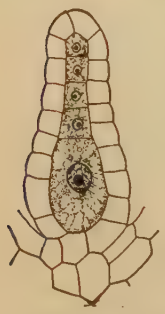

FIG. 28. — A developing archegonium of a liverwort (*Riccia*), showing the axial row.

probably indicating that there were formerly in the history of the archegonium two or more rows of gamete-forming cells within the sterile jacket. In any event, the fact of the transformation of the gametangium of algae into the archegonium of liverworts as a result of exposure to aerial conditions seems to be well assured.

FIG. 29.—The antheridium of a pine, represented by cells (or nuclei) developed within the pollen grain; in the figure, the pollen tube has begun to develop, and one of the antheridial nuclei has passed into it.

The archegonium is a very characteristic and persistent organ, changing comparatively little throughout its whole history. So constant is it that the groups which develop it, namely, the bryophytes (liverworts and mosses), pteridophytes (ferns, club mosses, etc.), and gymnosperms (conifers, etc.), are called collectively archegoniates, as distinguished from the thallophytes (algae and fungi) below, and the angiosperms (flowering plants) above, which do not have archegonia. This is an evidence of the remarkable adjustment of the archegonium as a sex organ suitable for land plants. The same statement may be made in general in reference to the antheridia that accompany the archegonia through most of the archegoniates. They vary more in details of development than do the archegonia,

but they are always of the same general structure, namely, a jacket of cells inclosing a mass of sperm-forming cells.

Changes begin to occur in the antheridium and its sperms, however, long before they begin in the archegonium. Through bryophytes and pteridophytes the antheridia retain the character described above, but in gymnosperms there is a decided change. In this group the male plant has become so dependent and reduced in size that it is permanently inclosed within the spore (pollen grain) that produces it (Fig. 29). In this position the jacket of sterile cells investing the antheridium disappears, for the antheridium is invested by the heavy wall of the pollen grain. The sperms are also reduced in number to two. In all the primitive gymnosperms these sperms persist as swimming cells, although the opportunity for swimming is very limited; but in the greatest living group of gymnosperms (the conifers) the sperms have lost their cilia, and are simply passive cells, carried to the eggs by outgrowths from the pollen grains, called pollen-tubes. It is in gymnosperms, therefore, that the antheridium passes into its third

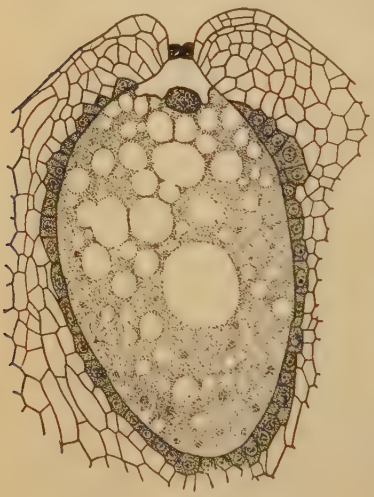

FIG. 30.—The achegonium of a pine, developed within the ovule.

stage, which is one of reduction in structure, of reduction in number of sperms, and of loss of motility by the sperms.

The archegonium, on the other hand, retains its character well through the gymnosperms (Fig. 30), but begins its third stage, which is one of disappearance in the most advanced group of gymnosperms. This complete elimination of the archegonium, begun in gymnosperms, is a feature of all angiosperms (Fig. 31), and its cause is evident. Among the gymnosperms and angiosperms the female plant has also become dependent, and so reduced in size that it remains permanently inclosed within the spore that produces it, a spore formed within the ovule (which becomes the seed). It is by no means so much reduced as is the male plant, for its spore (*megaspore*) is much larger than the one (*microspore*) producing the male plant. Hence the female plant develops considerable tissue and well-formed archegonia. But, in connection with its complete dependence, it begins to develop archegonia earlier and earlier in its history, until finally eggs are matured before there is any tissue to develop the sterile jacket. In other words, the archegonium is reduced to

FIG. 31.—The embryo sac of an angiosperm, showing a naked egg (central cell of the group of three at top of figure), the archegonium having been eliminated.

its essential sexual structure, the egg, which means that the distinguishing feature of an archegonium, the jacket, has disappeared.

The three stages in the evolution of sex organs, therefore, are as follows: (1) unprotected gamete-producing cells associated with the water habitat; (2) jacketed organs (antheridia and archegonia) associated with the land habitat; and (3) final elimination of antheridia and archegonia, associated with the complete dependence and reduction of the male and female plants.

CHAPTER V

ALTERNATION OF GENERATIONS

In general, the consideration of this subject begins with the condition among plants in which the same individual produces both spores and gametes, and the spore and zygote produce the same kind of individual. In other words, there is just one kind of individual in a life cycle, able to reproduce in a variety of ways, but reproduction always resulting in the same kind of individual as to appearance and powers. Alternation of generations consists in the separation of spore-production and gamete-production, so that there are two kinds of individuals in a life cycle, one producing spores but not gametes; the other producing gametes but not spores. The former is called the *sporophyte* ("spore-plant"), and the latter the *gametophyte* ("gamete-plant"), and they alternately produce one another. That is, the spore produced by the sporophyte develops a gametophyte, and the zygote produced by the gametophyte develops a sporophyte. The individual with sex organs (gametophyte) may be called the sexual individual, and the one without sex organs (sporophyte) may be called the sexless individual. Alternation of generations, therefore, is the alternation of a sexual individual with a sexless individual in a life cycle. This means that it takes two individuals to complete a life cycle. The above statement is merely the usual definition of alternation of generations as it appears among

plants, but it does not take into account the underlying causes of the alternation.

There are cytological features in this alternation that are more fundamental than the appearance and behavior of the two kinds of individuals. As stated in a preceding chapter, the number of chromosomes in the nucleus is a constant feature of each kind of plant and animal. When two nuclei fuse in the act of fertilization, the nucleus of the zygote contains the double number of chromosomes, and this double number is passed on by successive cell divisions until it is reduced again, which in plants usually occurs in connection with spore-formation. This means that in the life history of a plant in which sexual reproduction takes place, the chromosomes occur in two numbers. For convenience, these two numbers are usually indicated as x and $2x$. Tracing the chromosome situation through the life history of a plant, the following facts appear.

The zygote or fertilized egg is, of course, a $2x$ cell. In the alternation of generations the zygote produces the sporophyte, which is therefore a $2x$ individual. When the sporophyte produces spores the reduction of chromosomes occurs, so that the spores are x cells. In the alternation of generations the spore produces the gametophyte, which is therefore an x individual. For this reason, the sporophyte is usually spoken of as the $2x$ generation and the gametophyte as the x generation. It follows that $2x$ cells belong to the sporophyte and x cells to the gametophyte; therefore, the zygote is the first cell of the sporophyte, and the spore is the first cell of the gametophyte.

If the chromosome test be applied in determining the two generations, it becomes obvious that alternation

of generations begins with the appearance of sex, for every sex act results in a $2x$ zygote, and this means that somewhere in the life history a reduction to the x number must occur. If only one kind of individual occurs in a life cycle, as described at the beginning of this chapter, and this individual is produced alike by spores and zygotes, there are two alternatives. One alternative is that the individual is $2x$, in which case the reduction occurs in the formation of gametes, and the gametes are the only x cells in the life history. The other alternative is that the individual is x, in which case the reduction occurs at the division of the zygote, and the zygote is the only $2x$ cell in the life history. In the former case, the gametophyte is represented only by the gametes; while in the latter case the sporophyte is represented only by the zygote. Among animals, the only x cells in the life history are the gametes, so that the animal body corresponds to the sporophyte generation among plants, so far as the number of chromosomes is concerned, although it produces gametes and does not produce spores. The same thing is true of some plants, as the rockweed (*Fucus*), the reduction occurring in gamete-formation, and therefore the body is $2x$, a sporophyte body so far as the chromosome test goes. In both these cases, namely, animals and the rockweed, spores are eliminated, and this seems to be associated with reduction at gamete-formation.

Among plants, however, alternation of generations expresses itself more conspicuously than by an alternating number of chromosomes. It must not be forgotten, however, that this alternation in the number of chromosomes, made imperative by the appearance of sexual

reproduction, is the basis of alternation of generations, which in most plants comes to express itself in alternating individuals.

The simplest expression of alternation among plants, beyond mere alternation in the number of chromosomes, is shown by those algae whose zygotes do not produce individuals like those from which they come, but produce spores, which in turn produce new individuals. In other words, the zygote is a spore-producing body, which is really the definition of a sporophyte. In such plants, therefore, there are two sets of spores, one set produced in the ordinary way by the working body of the plant, and the other set produced by the zygotes. If the zygotes, instead of producing free spores, had produced a spore-forming structure, this structure would represent an individual different from the ordinary one, and alternating individuals would be evident.

The appearance of a sporophyte in a life cycle, therefore, is the appearance of a new individual produced by the zygote, which is prophesied by the sex act, begins to appear in spores formed by the zygote, and finally becomes a spore-forming individual produced by a zygote. This means that the older individual historically in the alternation is the gametophyte, which finally eliminates spore-production, and the alternation in function becomes complete.

Among some of the red algae, alternation of generations has reached an advanced stage, for the spore-bearing individual produced by the zygote is as conspicuous as the gametophyte. In fact, the alternating individuals resemble one another so closely that they are recognized only by the organs they produce.

In some cases there may be three individuals involved in this alternation; namely, an individual bearing male organs, another bearing female organs, and a third bearing sporangia. The male and female individuals together produce the zygote, which produces the spore-bearing individual, whose spores produce the male and female individuals.

The variable expression of alternation among the thallophytes, ranging from alternating numbers of chromosomes to distinct alternating individuals, passed into an established and obvious alternation with the appearance of the liverworts, the first land plants. It is usually stated that alternation of generations became established among the liverworts, but it must be understood that this refers to obvious alternation, for alternation really became established when sex was established. It is probably true that the land habit, with its much more variable conditions, emphasized alternation and made the alternating individuals differ. A brief consideration of the situation will explain this statement. The favorable condition for the gametophyte is moisture, so that fertilization may be accomplished by swimming sperms; while drier conditions favor the sporophyte, with its aerially dispersed spores. The spores are produced, therefore, in conditions of relative dryness, but they germinate in moisture, which is the condition for gametophyte development and functioning. Alternating conditions of dryness and moisture, therefore, would favor these alternating individuals, and make them more and more unlike.

An outline of the life history of a moss, which is the same as that of a liverwort, will serve to fix clearly in

mind the beginning of alternation in land plants (Fig. 32). The ordinary green moss plant produces antheridia and archegonia, but no spores, and therefore is a

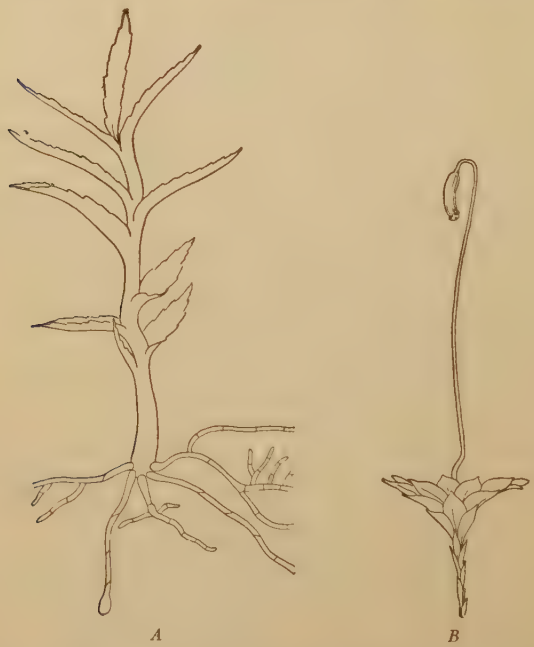

FIG. 32.—Life history of a moss: *A*, the young gametophyte produced by the spore, and which later produces sex organs; *B*, the sporophyte (spore case with long stalk) which is produced by the fertilized egg within the archegonium.

gametophyte. When the egg is fertilized in the archegonium, it begins to germinate immediately, but the individual it produces is quite unlike the ordinary moss plant. It seems to be nothing but a stalked spore-case, which anchors itself in the moss plant and looks as

though it were growing out of it. In fact, it is commonly spoken of as a moss "fruit," which of course it cannot be, since it is produced by an egg, and has no more connection with the moss plant than a superficial parasite has with its host. Since it produces an abundance of spores, but no sex organs, it is obviously the sporophyte, which is also proved by its origin from a zygote. The spores produced by this sporophyte give rise to moss plants (gametophytes), and the life cycle is complete. The facts to emphasize in this life history are that the gametophyte is an independent, food-forming plant, and the sporophyte is a dependent, living as a parasite upon the gametophyte. Among land plants, therefore, the sporophyte begins as a dependent and relatively inconspicuous individual, so dependent that it was long mistaken for a part of the gametophyte. And yet, it is upon this sporophyte that the future development of the plant kingdom depended. For this reason, it is important to consider its progress among bryophytes (liverworts and mosses).

The simplest sporophyte among liverworts is nothing but a simple spore-case anchored on the body of the gametophyte (Fig. 33); that is, it is a spherical body consisting of a single layer of jacket cells, inclosing a mass of spore-producing cells (*sporogenous tissue*). In advancing through liverworts, however, a gradual change in the structure of the sporophyte appears. Fewer and fewer cells of the sporophyte body function as spore-producing cells (Fig. 34). This is often spoken of as the "sterilization" of sporogenous tissue, meaning simply that cells formerly functioning as spore-producing cells cease to function in this way. As a result of this

change, the sporophyte body began to consist of two distinct regions, namely, sporogenous tissue and sterile tissue, the latter increasing at the expense of the former. There followed a differentiation into body-regions, the sterile tissues forming a more or less elongated stalk, and the sporogenous tissue being included in a region

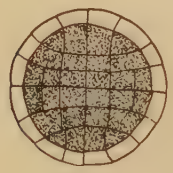

FIG. 33

FIG. 34

FIG. 35

FIG. 36

FIGS. 33–36.—Diagrams illustrating the evolution of the sporophyte among bryophytes: Figs. 33–35, liverworts; Fig. 36, moss.

of the body called the *capsule* (Fig. 35). The progress through liverworts and mosses simply emphasizes this differentiation of tissues and resulting body-regions. As a consequence, one finds in the higher mosses a sporophyte body consisting of an elongated stalk and a very elaborate capsule, while the sporogenous tissue within the capsule is reduced to a very small amount (Fig. 36). This progress of the sporophyte through

bryophytes has been designated "progressive sterilization," and its general result was to increase sterile tissue, by means of which a more and more complex body could be organized, and correspondingly to decrease sporogenous tissue, so that this tissue finally came to be a very insignificant part of the body in amount, and appeared only relatively late in the development of the body. The whole impression one gets from this progress is that the sporophyte is developing more and more as a distinct individual, with body-regions and organs.

The most important fact in the history of the sporophyte through the bryophytes, after the general fact of progressive sterilization, is that the sporophyte of certain liverworts began to achieve independence. In most bryophytes the sporophyte is absolutely dependent upon the gametophyte, but the sporophytes of the liverworts referred to develop green tissue, which means that, although they are anchored in the gametophyte and secure food from it, they are still able to manufacture food for themselves. If these green sporophytes could establish connections with the soil they would become absolutely independent, and cease to belong to bryophytes. The future of the sporophyte, therefore, was to achieve independence from the gametophyte, and this independence was begun by this group of liverworts and established by the pteridophytes.

Before describing the great change in the character of sporophytes and gametophytes among the pteridophytes, it may be well to consider what may be called the failure of bryophytes, since it probably has something to do with the modifications of the two generations that characterize the pteridophytes. By failure

of the bryophytes is not meant their failure as a group, for they are so very abundant that they must be called successful. The failure referred to is that the bryophyte plan could not make any further progress leading to higher plants. We infer that this is true simply because the plan of the higher plants is different.

In the more advanced liverworts and in mosses the archegonia and antheridia are more or less stalked above the general surface of the body. The advantage of this is seen when one remembers that the fertilized egg, thus carried up above the general surface, produces the sporophyte with its spore-case, and the spores are thus in a very favorable position for dispersal by air. If this position favors the spores, however, it does not favor the sperms, which must swim, for they are carried up into a position of least moisture. It is a remarkable arrangement that favors spores by interfering with the very act (fertilization) that results in spores; but it works reasonably well for plants living in moist situations. It is evident, however, that still larger and more leafy plants would interfere with the swimming of sperms still more. The three things which enter into this problem are food manufacture (which means display of green tissue to light and air), fertilization (which means water for swimming), and spore-production (which means exposure for air dispersal). In the bryophytes, food manufacture and fertilization belong to the gametophyte, and the condition that favors the one hinders the other. In other words, they are contradictory in their demands. On the other hand, food-manufacture and spore-dispersal make the same demands for exposure, and therefore they can be coupled together

to advantage. The further progress of plants, therefore, demanded that the spore-producing generation (sporophyte) should also become the food-manufacturing generation; and that the gametophyte, with its peculiar need for free water, should be restricted to fertilization. In the higher plants, therefore, the sporophyte is the conspicuous, leafy, independent generation, and the gametophyte is so very inconspicuous that it is only seen by those who know where and how to look.

The greatest break in the history of plants occurs between the bryophytes and pteridophytes (ferns, club mosses, etc.), so that the details of sporophyte advancement are lacking. However, we have seen that the sporophyte of certain liverworts attains partial independence, and the advancement of the sporophyte of pteridophytes is that its independence is complete. An independent sporophyte means one that can manufacture its own food, and this means that it is a green plant. This association of food-manufacture with spore-production combines functions that are favored by the same conditions of free exposure to the air. Correlated with the complete independence of the sporophyte is the much reduced display of the gametophyte. It no longer supports the sporophyte and is restricted to the function of gamete-production. So inconspicuous has it become in pteridophytes that for a long time it escaped observation, and the sex organs of ferns were unknown. The older botanists felt that sex organs must exist, although undiscovered, and so they named the group "Cryptogams" ("hidden sex organs").

The independent sporophyte deserves a brief consideration. It involves the appearance of three new

structures, the details of whose origin are left to the imagination.

The most significant new structure is the vascular system, a system of special water-conducting vessels. The name is in danger of suggesting an open system of tubes, like the vascular system of animals, but the water-conducting vessels of plants are special cells, arranged end to end to form strands, and in traversing them water must pass through innumerable partitions. The significance of this vascular system should be appreciated. Of course, water moves through the body of a moss, although there are no vessels, but it is the ordinary movement that may occur from any living cell to an adjacent one. The vascular system is a system of dead cells, through which water moves with greater rapidity and precision than through living cells. The difference in the freedom of movement of water in the two cases may be compared to the difference between water working its way through a swamp and water flowing in a definite channel. The chief significance of the vascular system, however, lies in the fact that it makes larger plant bodies possible. Probably the larger mosses represent the extreme size of a plant body that is possible without a vascular system; but with a vascular system even large trees are possible. It must be remembered that the plant body, to be in good working condition, must be kept saturated with water, and that the larger the plant body, the greater is the exposure to loss of water by evaporation. To meet all this loss and keep the body full of water necessitates a special water-carrying system. The origin of the vascular system, like the origin of all structures in

which the pteridophytes differ from the bryophytes, must be left to speculation. In the stems of the larger mosses there are elongated cells which facilitate the movement of water, and this is the only hint we have as to the way in which the vascular system may have started in the sporophyte; it certainly never developed in the gametophyte.

Two other new structures of pteridophytes are implied by the presence of the vascular system, namely, roots to receive the water supply from the soil, and leaves to which the water supply is chiefly carried. A vascular system would be meaningless without roots and leaves. Leaves are not new structures in the plant kingdom, for mosses and many liverworts have leaves, but among pteridophytes we meet the first leaves produced by a sporophyte.

A summary of the contrast between the sporophyte of pteridophytes and that of bryophytes, from which it seems to have been derived, may be stated as follows: The sporophyte of bryophytes is a leafless, dependent plant, without vascular system or roots; while the sporophyte of pteridophytes is a leafy, independent plant, equipped with a vascular system and roots. In other words, the conspicuous fern plant is the equivalent, not of the conspicuous moss plant, but of the moss sporecase. This means that when one speaks of a fern he is referring to the sporophyte; while in speaking of a moss he is referring to the gametophyte.

This large and independent sporophyte involves a situation that concerns the evolution of the sexual individual (gametophyte). Correlated with a larger vegetative body is the later appearance of sporogenous tissue.

This means that spores are formed at the period of waning vegetative activity, much as gametes were formed in the early history of sex. If spores appear in conditions relatively unfavorable to vegetative activity, they will either pass into the dormant stage, in which case they will germinate when favorable conditions are beginning to return, or they will germinate immediately. In either case the conditions for maximum vegetative activity are not present, and the result will be a relatively small body. For this reason the gametophytes of pteridophytes may be expected to be "reduced," as compared with the more vigorous gametophytes of bryophytes. In other words, the active and vigorous sporophyte has pushed spore-formation to the end of the growing season. On the other hand, the fertilized egg functions after conditions for vegetative activity are present, and there is no inhibition of the development of a sporophyte with a vigorous body. This tendency for the gametophyte to become more and more inconspicuous after the sporophyte has become independent is very marked throughout vascular plants.

The life history of an ordinary fern will summarize the alternation of generations as expressed by the pteridophytes. When a spore germinates, it forms a very small gametophyte, so inconspicuous that it long escaped discovery (Fig. 37). This minute body (generally called a *prothallium*) is green and independent, resembling a tiny flat liverwort. Unlike the liverwort, however, the sex organs are not produced from the upper surface, but from the lower surface, against the substratum. The significance of this position is apparent

when it is remembered that the swimming sperms must find a water medium. There is no place in the land plant where a film of water is more likely to occur than between a prostrate body and its substratum. The

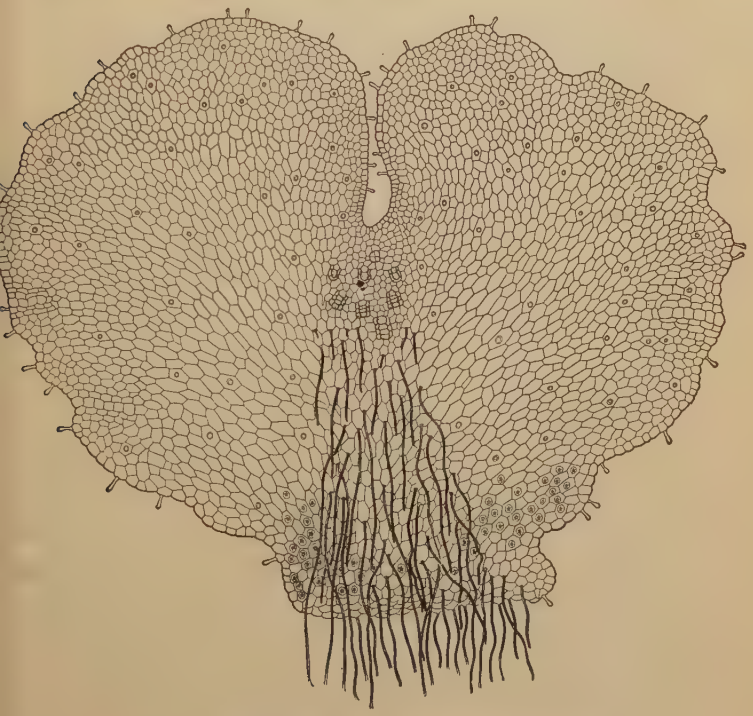

FIG. 37.—The prothallium (gametophyte) of a fern.

failure of bryophytes in this particular, in carrying their sex organs up into the air, is thus avoided by the pteridophytes, so that fertilization in the latter is a much more constant feature in the life history than in the bryophytes, especially the mosses.

The fertilized egg, within the archegonium imbedded in the under surface of the gametophyte, germinates immediately and produces the strong sporophyte, which very soon becomes independent by the development of

FIG. 38.—Under surface of fern leaves, showing groups (sori) of sporangia.

roots and leaves, emerging from beneath the gametophyte, and sending its shoot, or at least its leaves, upward. At its maturity, the sporophyte produces spores (Fig. 38), which in turn produce gametophytes, and the alternation is complete.

The next stage in the evolution of the two alternating generations is introduced by the appearance of *heterospory*, a situation developed by certain pteridophytes, notably by some of the club mosses, and referred to briefly in a preceding chapter. Up to this point, all spores have been alike in their appearance and product, each one producing a gametophyte which bears both antheridia and archegonia. Heterospory means that the spores are unlike, and this differentiation of spores should be understood. A sporangium produces either a large number of small spores, or a small number of large spores. Since the available material for spore-production is the same in both cases, the size of the spores depends upon the number produced. Heterospory seems to have arisen by restricting the number of spores in certain sporangia, and as a consequence increasing their size. This restriction has been seen in a number of cases to consist in inhibiting all of the numerous sporogenous cells within a sporangium excepting one, which then grows at the expense of the others, and forms four large spores. The small spores are called *microspores* and the larger ones *megaspores* (Fig. 39).

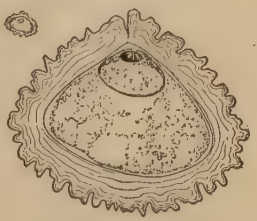

FIG. 39.—A megaspore and microspore of a club moss (*Selaginella*) drawn to same scale.

Difference in size, however, would be of little importance if it did not involve difference in function. The important fact connected with heterospory is that the megaspores produce female gametophytes and the microspores produce male gametophytes. With the appearance

of heterospory, therefore, gametophytes become sexually differentiated, so that two gametophytes are involved in the alternation of generations. The importance of this fact is indicated when it is known that heterospory, although begun in pteridophytes, is characteristic of all seed plants. In fact, heterospory made seed plants possible.

That large spores should produce female gametophytes and small ones male gametophytes is evident when the relation of the two gametes to food supply is remembered. Only a well-developed body can produce the highly nutritive egg, while a much smaller body can produce sperms. While a well-nourished gametophyte might produce sperms early in its development and eggs at its maturity, as is actually the case among ferns, a poorly nourished gametophyte could not produce eggs. Differentiation in the size of spores, therefore, naturally results in the sexual differentiation of individuals.

The effect of heterospory upon the gametophytes is seen not only in the sexual differentiation of individuals, but also in the dependence of the gametophytes. Up to this time, the gametophyte has been an independent plant, existing before the sporophyte appeared, nourishing the sporophyte among bryophytes, and maintaining its independence by the side of the large and independent sporophyte of pteridophytes. But with the appearance of heterospory, the gametophyte becomes entirely dependent, a parasite upon the sporophyte. When the two kinds of spores germinate, the gametophytes are so small that they remain within the spores that produce them. Of course the female gametophyte makes much

more tissue than does the male gametophyte, but it remains within the megaspore inclosure. The gametophytes, therefore, have not only become much reduced and dependent, but they have disappeared from ordinary observation. In heterosporous plants, therefore, the sex organs can only be discovered by the use of laboratory technique.

The condition of the two generations in seed plants must be considered, since it not only follows their history to its completion, but also corrects certain very common and very natural misapprehensions. Heterospory not only differentiates spores, but also sporangia, so that those producing megaspores are called *megasporangia*, and those producing microspores are called *microsporangia*. The product of the two is so different that they soon become quite unlike in their appearance. Furthermore, the sporangia are usually produced by leaves, and such leaves gradually become more and more unlike ordinary leaves, until soon they do not resemble them at all. Such special sporangium-producing leaves are called *sporophylls*, and naturally those producing megasporangia are called *megasporophylls*, and those producing microsporangia are called *microsporophylls*. It will help to make the following discussion clear to remember that megasporophylls produce megasporangia, which produce megaspores; and that microsporophylls produce microsporangia, which produce microspores.

The gymnosperms are the primitive group of seed plants, their origin from the ferns having been established. In fact, the luxuriant fernlike vegetation once thought to be a feature of the Coal Measures has turned out to have been fernlike gymnosperms. That these

fernlike plants were gymnosperms and not ferns is shown by the fact that they bore seeds.

In the modern gymnosperms the sporophylls form the characteristic cones. There are two kinds of cones, the conspicuous ones being composed of megasporophylls. For example, it is this megasporangiate cone that is ordinarily observed on a pine tree, the much smaller microsporangiate cones usually escaping observation. These cones are often spoken of as "male" and "female" cones, names which are obviously misapplied, since sporophylls are structures belonging to a sporophyte. Each megasporophyll (often called scale) of a cone bears one or more megasporangia. These megasporangia were called *ovules* long before their real nature was known, and the megasporophyll was called a *carpel* or *pistil*. Within each megasporangium (ovule) a large megaspore is developed. This megaspore is never shed, but germinates within the ovule, forming the female gametophyte with its archegonia and their eggs. The ovule (megasporangium), therefore, contains the female gametophyte as an internal parasite, and it is this relation that results in transforming such an ovule into a seed. A seed, therefore, is a transformed megasporangium with its contents. The female gametophyte was observed long ago imbedded in the ovule as a tissue very distinct from the rest of the ovule, but it was thought to be simply a special nutritive tissue of the seed, and it was called first *albumen* and later *endosperm*. The latter name is still used as more convenient than female gametophyte.

Each microsporophyll of a cone bears several microsporangia, which contain microspores. Before the real

nature of these structures was known, the microsporophyll was called a *stamen;* the region of the microsporophyll bearing sporangia was called an *anther;* the microsporangia, *pollen sacs;* and the microspores, *pollen grains*. The abundant microspores (pollen grains) are shed and are scattered widely by the wind, the successful ones falling upon the megasporangiate cones. In germination, the microspore produces so small a male gametophyte that it consists of only a few cells which remain inclosed by the spore, until the sperms are discharged into the archegonia within the ovule.

It is no wonder that such gametophytes were not observed, and that the sporophylls (stamens and pistils) should have been regarded as sex organs. The name "ovule" suggests that it was thought to be an egg; it certainly did not suggest a sporangium to those who had not followed the history of the ovule. It is evident that sporophylls produced by sporophytes cannot be sex organs, but their behavior indicated that in some way they were connected with the sex act.

In the true flowering plants (angiosperms), the great group of seed plants and the culminating group of the plant kingdom, the same conditions are carried forward to a greater extreme. The two sporophylls (stamens and pistils) become so different from ordinary leaves as hardly to suggest them, and they become a part of a new structure called the *flower*. The flower is nothing but the cone of gymnosperms, composed of sporophylls, accompanied by new kinds of leaves (*sepals* and *petals*).

In angiosperms the male gametophyte is reduced to its lowest terms, being represented by only three cells, two of which are sperms, and the antheridium as a definite

organ has disappeared. The passive sperms are carried to the egg, deep within the ovule, by a penetrating pollen tube. The female gametophyte is also reduced to its lowest terms, being represented by only a few free cells at the time of fertilization, one of the cells being the egg. This gametophyte is so reduced, that is, so little developed, that there is no tissue for the development of archegonia, so that the female sex organ is also eliminated.

It is obvious that to regard a flower as a sex structure and its stamens and pistils as sex organs is to misapprehend the situation. They belong to the sporophyte, which does not produce sex organs. But the stamens and pistils contain the spores that in germination produce male and female gametophytes. To speak of male flowers and female flowers, as is so often done, is natural, but it is untrue.

The general history of the two generations, sporophyte and gametophyte, may be summarized very briefly. The gametophyte begins in the thallophytes as the only individual; it continues in the bryophytes as the conspicuous and independent individual; it appears in the pteridophytes as an inconspicuous but still an independent individual; while in the seed plants it disappears entirely from ordinary observation and becomes a dependent, internal parasite. The history of the sporophyte exactly reverses this. It appears in the bryophytes as a fully established individual, but relatively inconspicuous, and entirely dependent upon the gametophyte; in the pteridophytes it has become a conspicuous and independent individual; while among the seed plants it is the only individual seen (Fig. 40).

A situation is developed in the angiosperms that needs explanation in connection with the history of sex. The appearance of heterospory would seem to indicate that by the separation of sexes in the differentiation of the gametophytes, some physiological benefit was obtained. It is assumed in general that the fusion of a sperm and an egg from two individuals secures a more vigorous progeny than when the sperm and egg are from the same individual. This means that, within limits, a difference in origin of sperm and egg is an advantage

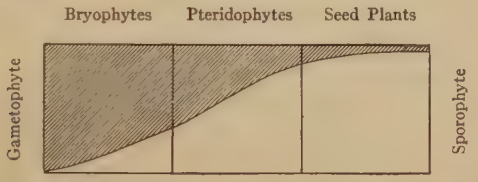

FIG. 40.—Diagram illustrating the advance of the sporophyte and the decline of the gametophyte.

in reproduction. It is a notable fact that, in general, hybrids are likely to be more vigorous than either parent. In angiosperms, however, while of course the two gametophytes are separate, they are brought together upon the same sporophyte in every flower containing both stamens and pistils. Whatever physiological benefit, therefore, came from their separation in the early history of heterospory is counteracted by bringing them together again to depend upon the same individual (sporophyte). In gymnosperms the gametophytes are separated by being developed in different cones, and these cones are often upon different plants.

There are also many angiosperms which have pistillate flowers on one plant and staminate flowers on

another. Of course in these cases the physiological advantage of separating male and female gametophytes is maintained. But in the majority of angiosperms the flowers contain both stamens and pistils, and therefore the two gametophytes depend upon the same individual for their nutrition. The advantage lost by the sexual separation is offset in this case by the elaboration of devices for cross-pollination. It is among angiosperms that insect-pollination has reached so great a degree of development that the female gametophyte, developed within the ovule of one flower, seldom mates with a male gametophyte developed in a pollen grain of the same flower. In other words, the mating gametophytes are developed in connection with different sporophytes.

Before concluding this discussion it may be well to emphasize the real nature of a seed. There is no plant structure more commonly observed or more commonly studied, and at the same time so poorly understood. From what has been said above, it is evident that in a certain sense a seed is a transformed megasporangium. Its transformation consists in changes that follow the act of fertilization. It will be remembered that the ovule (megasporangium) consists of the ordinary tissues of a sporangium, within which a megaspore is imbedded; and within the megaspore is the female gametophyte with its egg. When this egg is fertilized by the sperm that has been discharged into the megaspore cavity, it begins to develop the embryo. At the same time, changes occur in the superficial tissues of the ovule, resulting in the development of a hard seed coat. When this coat has been completely organized, the development of the embryo is checked, and it passes into that dormant

condition which is familiar in the case of a seed. In fact, therefore, the seed has locked up within its structure the representatives of three generations. The seed coat and more or less of the tissues beneath it, which have been derived from structures of the sporangium, represent the old sporophyte; the endosperm within represents the female gametophyte; while the embryo is the sporophyte of the next generation (Fig. 41). It is really surprising to realize how many seeds are studied with no appreciation as to their real nature.

FIG. 41.—Seed of violet: the left figure shows the hard seed coat; the right figure the abundant endosperm (female gametophyte) inclosing the embryo (young sporophyte).

Another very common misapprehension may be explained in this connection. Nothing is more common than to speak of the "germination" of a seed, and not very far back in the history of botany seeds were contrasted with spores. In fact, the plant kingdom was divided into plants that reproduce by seeds and those that reproduce by spores. It was very natural to infer that, since spores germinate to produce new individuals, seeds are doing the same thing. It is evident, from what has been said, that the germination that starts the new seed plant is the germination of the fertilized egg, which begins almost immediately after fertilization to form the embryo. This embryo passes into the dormant stage. When so-called "germination" of the seed occurs,

therefore, it is merely the arousing of this dormant embryo to activity and its escape from the seed coat. Seed germination does not result in the production of a new plant, for the new plant has already been produced and is within the seed. It simply results in giving the new plant an opportunity to escape and continue its development.

CHAPTER VI

DIFFERENTIATION OF SEXUAL INDIVIDUALS

We have considered the *origin of sex*, concluding that gametes are the lineal descendants of swimming spores; the *differentiation of sex*, resulting in visibly distinct eggs and sperms; and the *differentiation of sex organs*, leading to the appearance of gamete-producing organs as special appendages of the working body. All of these results have appeared as responses to the varying conditions of plant life. These conditions have not been analyzed fully, and important factors have doubtless been overlooked, but the general situation seems to be that the rise and fall of vegetative activity is responsible for much of this differentiation.

It remains now to consider the appearance of male and female individuals as the extreme expression of sexual differentiation, a differentiation that involves more than the differentiation of male and female gametophytes, with their male and female sex organs. That this is the final achievement of sex is indicated by the fact that all seed plants and all higher animals show this differentiation. And yet, sexual individuals appear here and there throughout the whole history of sex, becoming finally established as a constant feature only in the higher forms. A consideration of the occasional appearance of male and female individuals among the lower forms should lead to some conclusions.

Spirogyra, already used as an illustration of the differentiation of gametes, illustrates also the early

appearance of male and female individuals. It is often the case that one of the pairing filaments discharges all of its protoplasts into the other filament (Fig. 42). The discharging filament is evidently male and the receiving filament female, although the gametes, which are transformed vegetative protoplasts, do not differ in appearance. That there is a difference is evident because one of the gametes moves and the other remains passive, although both seem free to move. In the transformation of vegetative protoplasts into gametes, therefore, the two pairing gametes have become unlike, and this unlikeness characterizes all the gametes of the two filaments. It is impossible to imagine, in this case, that the external conditions for development are different for the two filaments, for they are lying side by side. It must be something in the constitution of the two sets of protoplasts that differs, resulting in "maleness" in the one case and "femaleness" in the other. These are words rather than explanations, but they stand for a definite physiological difference. In this case there is no apparent difference in the vigor of the two filaments, which is so often associated with the difference in gametes, nor would this be expected in *Spirogyra*, since the two gametes are alike in bulk. Difference in nutritive power has to do with the difference of the gametes in bulk, and difference in bulk is due to difference in the

FIG. 42.—An alga related to *Spirogyra*, showing male (empty) and female (with zygotes) filaments (individuals).

amount of cytoplasm. Maleness and femaleness, therefore, have to do with differences in the constitution of the nuclei, which may of course involve secondary differences in the cytoplasms also. In the male and female individuals of *Spirogyra*, therefore, all of the protoplasts of a filament are of the same sexual constitution.

Not all of the species of *Spirogyra* exhibit this differentiation, for in some cases each of the pairing filaments both discharges and receives. The cells are sexually differentiated, but not the individuals. In this case the sexual constitution of all the protoplasts of a filament is not the same, and yet all of the cells have descended from a single parent cell, the zygote. The zygote, however, is the one cell in the whole life history whose nucleus is the direct combination of male and female nuclei. When it produces a new individual, the male and female characters are either distributed among the cells, in which case the filament will both discharge and receive gametes; or one of the sex characters is inhibited, in which case the filament as a whole either discharges or receives gametes, that is, it is either a male or female individual. At this stage of our knowledge it is useless to ask what "maleness" and "femaleness" are, but it seems evident that they represent essentially conditions of the nucleus; that they coexist in a zygote; and that one or both may be expressed in the new individual in the organization of gametes. This seems to indicate that every vegetative protoplast of *Spirogyra* contains the sex-determiners, and that in this sense the whole individual is sexual.

Another filamentous green algae, *Oedogonium*, exhibits other details in the appearance of male and female

individuals. Its active vegetative cells become transformed into sex organs, the solitary egg being formed in an enlarged, spherical cell (oögonium), and the sperms being formed in cells (antheridia) smaller than the ordinary vegetative cells (Fig. 43). In fact, antheridia are vegetative cells which have not enlarged after division. Here there is a great difference in the nutritive capacities of the cells that produce eggs and sperms, but maleness and femaleness are both present in the same individual. There also remain in the filament vegetative cells that do not become sex organs, but the conclusion is inevitable that their nuclei are also male and female.

FIG. 43.—Sex organs of *Oedogonium:* the large cell (oögonium) contains the egg; the two small cells (antheridia) have just discharged sperms.

In certain species of *Oedogonium*, however, there are male and female individuals, but they are very far from being alike in vigor. The ordinary vigorous filament produces only oögonia, so that the first impression would be that all of its cells are female. The male filament is a very small dwarf, plainly incapable of producing bulky eggs, but producing sperms (Fig. 44). The origin of these dwarf males is suggestive. The vigorous filament produces two kinds of spores: large spores which produce vigorous filaments with oögonia; and much smaller spores which produce dwarf males. Not all of the protoplasts

of the vigorous filament, therefore, are female, although as an individual it produces only oögonia, for those protoplasts forming the smaller spores are evidently male, for they produce males. It follows, therefore, that an individual sexually differentiated so far as its sex organs are concerned, and therefore to be called in the case of the large *Oedogonium* filaments a female individual, may not be sexually alike throughout its body.

FIG. 44.—An alga related to *Oedogonium*, showing a dwarf male filament attached to an oögonium.

If it were not for *Spirogyra*, one might conclude that the maleness of the *Oedogonium* dwarf is due to lack of nutrition, and that the femaleness of the vigorous filament is due to abundant nutrition; but, as has been shown, this difference of nutrition is correlated with the relative bulk of the two gametes, and not with their sexual character. The more logical conclusion in the case of *Oedogonium* is that male and female characters coexist in all the protoplasts, and that lack of nutrition may be one of the conditions that inhibits femaleness from expressing itself, and permits maleness. It would follow that a female individual, for example, is both male and female in nuclear constitution, and female only in function. That there is some other condition besides nutrition inhibiting one sex and permitting the other is indicated by *Spirogyra*, where the nutritive supply of both gametes is the same. This differentiation of the

individuals of *Oedogonium* into male and female, related to the size of the spore producing the individual, is interesting incidentally as an early case of heterospory, long before it becomes an established fact among plants.

The molds (mucors) also indicate that the selection of the functioning sex depends upon something more than the amount of available nutrition. In these fungi the details of the sex act resemble those of *Spirogyra* in that conjugating tubes are developed by two adjacent individuals and meet in pairs (Fig. 45). In this case, however, the pair of meeting tips are cut off by walls from the rest of the body and function as gametes, forming a zygote. In most cases the gametes are alike in size and behavior, and for a long time no distinction of sex was discovered. It was observed that the molds under ordinary observation very rarely produced zygotes. They continued in vegetative activity, and no change of conditions induced gamete-formation. Then it was discovered that the mycelia (the characteristic bodies of fungi) are distinctly male and female, although morphologically indistinguishable. When the two kinds of individuals are brought in contact, gametes are formed and zygotes are abundant. Then other

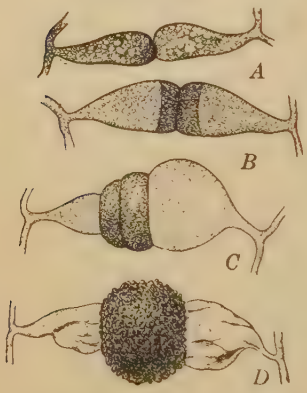

FIG. 45.—Sexual reproduction in the molds (*Mucor*): *A*, conjugating tubes in contact; *B*, the two sex organs (gametangia) cut off by walls; *C*, the two conjugating tubes and their gametangia unequal in size; *D*, the zygote.

molds were discovered whose pairing gametes differ in size, and the pairing individuals differ somewhat in robustness. The more robust bodies were traced in origin to larger spores. There is nothing to distinguish maleness from femaleness in this case except to assume that the more robust mycelium with the larger gamete is female. This again seems to relate femaleness to nutrition; but when there is no observable difference in the robustness of the pairing mycelia or in the size of the gametes, which is the usual condition, the sexual differentiation of individuals is just as distinct and persistent. The zygote, which of course contains both sex-determiners, produces a mycelium which is either male or female so far as gamete-formation is concerned, and this mycelium produces spores from which arise both male and female individuals. It is possible to imagine a differentiation of spores, so that male mycelia produce spores from which only male mycelia arise, and vice versa; but since all zygotes must be both male and female, this would simply refer all sex-determination to the germinating zygote, rather than share it with germinating spores. In either case, sex is a feature of the whole individual and not simply of the gametes.

The three plants described above point to certain conclusions in reference to sexual individuals. Whatever the differences between male and female gametes may be, they are inheritable as sex-determiners which can be transmitted through generations of vegetative cells, and do not originate *de novo* at gamete-formation. Both determiners may express themselves in the same body, or one of them may be completely inhibited. The different conditions which determine that certain

protoplasts of a body shall produce eggs and others sperms become peculiar to different individuals, and thus individuals are sexually differentiated. At the same time, a female individual contains the male determiners and can transmit them, and vice versa.

A visible accompaniment of this situation has been observed in certain animals and plants, which may be an index of the physiological reactions involved. The so-called *X* chromosome is an extra one beyond the characteristic number for the individual. This chromosome appears in all eggs and in approximately half the sperms. In the formation of a zygote, an egg may mate with a sperm having an *X* chromosome, or with one not having such a chromosome. The result is that the zygote contains either two *X* chromosomes, in which case it produces a female, or it contains only one, in which case it produces a male. In other words, it is the character of the sperm that determines the sex of the offspring. This is not an explanation, but an observed fact, which indicates that the selection of the sex-determiner, in the case of sexually differentiated individuals, is made in the organization of the zygote; but it does not suggest, in its present form, the mechanism in those cases in which the zygote produces a bisexual individual. The only thing that can be said is that whatever determines the sexual differentiation of cells in the bisexual individual also determines the differentiation of sexual individuals. A feature common to the whole individual may well be determined by the zygote; but features that differentiate the cells of an individual must be determined during the development of that individual.

In certain of the red algae (as *Polysiphonia*) the sexual differentiation of individuals is very marked, and the life history presents complications that deserve consideration. As has been described in a preceding chapter, in addition to the male and female individuals there are also spore-producing individuals, so that three different kinds of individuals are involved in the life history. All of these individuals are alike in vegetative appearance and vigor, and can be recognized only by the organs they produce. The spores produced by the spore-plant are all alike in appearance, but they produce male and female individuals. The spores, therefore, are differentiated as to sex-determination, and the individual producing them has received the determiners for both sexes, in that sense being bisexual, although producing no gametes. These spore-forming individuals are produced by *carpospores*, which are produced by a kind of spore-fruit, so that both sex-determiners have been transmitted through the spore-fruit into the carpospores. The spore-fruit has arisen in turn as the result of the sex act, and of course has received the sex-determiners directly from the two gametes. When one considers that the male and female determiners have passed through the cells of the spore-fruit into the carpospore; from the carpospore into the spore-producing plant; through the numerous vegetative cells of this plant into its spores, where they finally encounter conditions that determine the sexuality of the plants produced by these spores, he must conclude that both sexes are represented in some condition in all the cells of a plant, and that male and female cells, and male and female individuals, are simply the cells or the

individuals in which sex appears in definite structures and functions.

Among the bryophytes, with alternation of generations established, the independent gametophyte is either bisexual or unisexual. In the latter case, sex inheritance is practically the same as that of the red alga described above. That is, the spores produced by the sporophyte, although appearing alike, produce male and female gametophytes which are alike in appearance and vigor, indicating no relation between nutrition and sex-differentiation, so that sex seems to be determined in connection with spore-germination. The zygote (fertilized egg) produces the sporophyte, through whose succession of cells the sex-determiners pass to the spores.

The case of bisexual individuals, however, suggests another interpretation. In this case, every germinating spore produces a gametophyte that develops both eggs and sperms, and therefore sex is not determined in the spore, but in the developing gametophyte. The inference is that probably sex is never determined in spores, and always in the developing sexual plant. This means of course, that every plant produced by a spore receives both male and female determiners, and that in some cases both determiners function, and in other cases one of them is inhibited. Furthermore, among the bryophytes, even with their well-developed eggs, such inhibition seems to hold no relation to nutrition. At this point, the general conclusion is suggested that both sexes are represented potentially at every stage of a life history; that unknown conditions result in their expression in the form of functioning gametes; and that an unknown inhibitor prevents now one sex and now the

other from expressing itself. This is analyzing a problem rather than solving it.

It is among the ferns that a connection between sex and nutrition is suggested clearly. The very small bisexual gametophyte (prothallium) has been followed through every step of its development, and a definite relation between the appearance of antheridia and archegonia discovered. At the very earliest stage in the development of the gametophyte, in what may be called an embryonic stage, the antheridia begin to appear, while the archegonia do not begin to form until the gametophyte is well developed. As a consequence, the antheridia and archegonia are often grouped in different regions of the body, the former in the basal region, the latter in the apical. It is apparent that antheridia can be developed by a much more immature body than can archegonia, but a fact to be explained is the usual inhibition of antheridium-formation as the nutritive capacity of the body increases. If it is safe to conclude that increasing nutrition favors archegonium-formation, it is just as safe to infer that it also may inhibit antheridium-formation. There is no reason to doubt that here, as in the previous cases, both sex-determiners are represented throughout the prothallium; that the conditions favoring the two sexes are not the same; and that the inhibitor of sperm-formation is connected with the later history of the prothallium. As in many bryophytes, the fern spores produce bisexual gametophytes, so that the appearance of sex is determined in connection with development of the gametophyte. The large, leafy, vascular sporophyte has transmitted the sex-determiners from the fertilized egg to the spores,

so that a fern plant, although sexless, is a channel for sex, and all of its cells leading to the sporogenous tissue contain the possibilities of both sexes.

The scouring rushes (*Equisetum*) add their testimony as to the relation between sex and nutrition. Among the bryophytes the sexually differentiated individuals are alike in size, and arise from similar spores, while in *Equisetum* the sexually differentiated individuals are very different in size (Fig. 46), and yet the spores producing them are similar. This suggests that the nutritive supply of a spore holds no necessary relation to the size of the gametophyte produced. If the nutritive supply is necessarily related neither to differentiation of sex nor of size, one may at least regard it as a common accompaniment of such differentiations, a secondary feature. It might be inferred that the smaller gametophyte of *Equisetum*, being less vegetatively vigorous, cannot mature eggs; but it is just as reasonable to infer that it is smaller because it is male. In fact, *Equisetum*, with its equal spores, indicates that the male gametophyte is small because it is male, and not male because it is small.

With the establishment of heterospory, the sexual differentiation of individuals becomes permanent. Since heterospory appears among the pteridophytes, and is a constant feature of seed plants, in the life histories of all the higher vascular plants male and female individuals are involved, as well as a sporophyte. The origin of heterospory, therefore, is an important problem in connection with the history of sex. Since the megaspore produces the female gametophyte and the microspore produces the male gametophyte, the temptation is to

explain the sexual differentiation in this case by the differentiation in the nutritive capacity of the two gametophytes, and to explain this difference in nutritive capacity

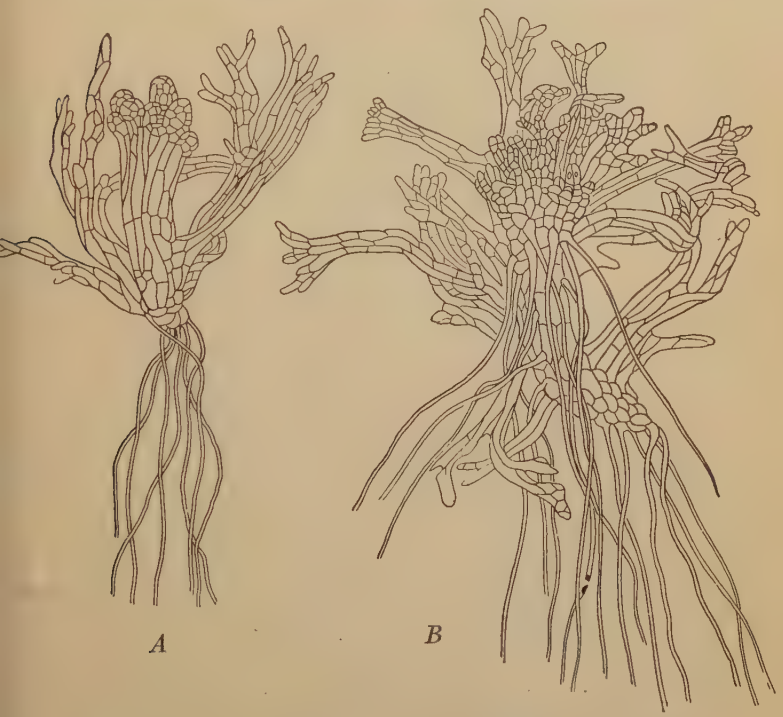

FIG. 46.—The male (*A*) and female (*B*) gametophytes of *Equisetum*.

by the difference in the size of the spores. Many bryophytes show us, however, that sex-differentiation does not depend upon different nutritive capacity, for equally vigorous gametophytes are sexually differentiated. Moreover, *Equisetum* shows us that differentiation in

the size of gametophytes does not depend upon the size of the spores producing them, for in this case spores of the same size produce unequal and sexually differentiated gametophytes.

The last case mentioned is not inconsistent with the fact that megaspores produce larger gametophytes than do microspores. In *Equisetum* the spores germinate in free conditions, the gametophytes being dependent upon the spores only for a start, and not for full development. In heterosporous plants, however, the microspore is the sole source of food supply for the male gametophyte; while the megaspore contains a very much larger food supply for the female gametophyte, and in seed plants this is supplemented by the ovule within which the megaspore germinates. It is inevitable, therefore, that the female gametophyte will be much larger than the male gametophyte, and of course with a much larger supply of available nutrition. The important question to consider is whether this difference in nutrition determines the sex of the individuals produced. If this were true, it would follow that in the sexually differentiated bryophytes referred to above, one of the gametophytes is male in spite of its vegetative vigor, and the other is female because of its vegetative vigor. The case of the fern prothallium suggests that male organs may be produced by an individual early in its development; that they are inhibited by a more fully developed body; and that female organs are developed only by a relatively matured body. If this program be applied to heterosporous plants, it would explain why the microspore produces a male gametophyte, but it would not explain why the female gametophyte does not produce male sex

organs early in its history. In other words, why is antheridium-formation inhibited in the case of female gametophytes? It seems evident, therefore, that the sexual differentiation of these two individuals depends upon something more than the amount of available nutrition. There seem to be two possible alternatives: the spores are either completely sexually differentiated, so that the sex of each gametophyte is inevitable; or the megaspore contains something that inhibits the production of antheridia by the developing female gametophyte. The latter alternative seems preferable, because it is consistent with the unbroken continuity of sex-determiners observed in the life histories described above, involving in the ferns, for example, their transmission through an extensive sporophyte. It is also more consistent with the facts involved in the life history of the dioecious sporophytes of seed plants, which bear staminate and pistillate flowers on different individuals. This means that one sporophyte produces megaspores and another microspores, which involves a sex-differentiation of sporophytes.

The difference between the two sporophytes of dioecious seed plants involves the same problem as the sexual differentiation of gametophytes. Why does one sporophyte produce only megaspores; and another of equal vigor, and in the same conditions, produce only microspores? The fact that sporophytes ordinarily dioecious are not always so, and that those ordinarily monoecious are occasionally dioecious, indicates that the ordinary conditions of differentiation may vary, and are not established when the sporophyte begins its development. In such dioecious plants, the fertilized egg

(zygote), which has certainly received both sex-determiners, produces either a megasporangiate sporophyte (one with pistillate flowers) or a microsporangiate sporophyte (one with staminate flowers). There is no apparent difference in the eggs to account for these very different results. The pistillate plant produced by the egg matures megaspores, which in germination produce female gametophytes; while the staminate plant produced by an egg of apparently the same constitution matures microspores, which in germination produce male gametophytes. The temptation is to imagine that in the germination of the egg, either only one kind of determiner is passed on, or, in passing both on, they are accompanied by an inhibitor for one of them. The occasional departure from the strictly dioecious habit here suggests the latter alternative.

An additional complexity is involved in the case of the dioecious seed plants. If a pistillate sporophyte contains only female determiners, or an inhibitor for the male determiners, this results not merely in the production of megaspores, but also in the development of all the structures related to megaspores, namely, pistils and pistillate flowers. In other words, the sex-determiner, being transmitted through the sporophyte to express itself later in the gametophyte, determines in the mean time the character of the flower.

After tracing the origin and history of sexual individuals among plants by means of the illustrations given above, taken to represent different situations and different plant levels, the complexity of the problem is apparent, but the facts point to certain tentative conclusions.

Gametes are necessarily differentiated physiologically, and whatever explains this differentiation will explain the differentiation of sexual individuals. It seems to be a differentiation in chemical and physical constitution, which may or may not express itself in bodies visible in the sexual cells.

Whatever may be the cause of sexual differentiation, it is capable of being transmitted through generations of vegetative cells, until conditions favor its expression in the form of gametes and their associated structures. The implication of this statement is that sexuality does not arise *de novo* when gametes appear, but that what have been called for convenience sex-determiners are always present in the plant body. These determiners are conceived of as representing substances that under appropriate conditions react in such a way as to determine the appearance and character of the sexual cell.

Along with sex-determiners there must be corresponding sex-inhibitors, for it seems clear that every protoplast contains both determiners, but gamete-forming protoplasts produce only one kind of gamete. It seems probable, therefore, that every gamete-forming protoplast is equipped with two determiners and one inhibitor.

In the early history of sex, the protoplasts of an individual differ as to this equipment, so that the individual is bisexual, so far as gamete-formation is concerned. Later, all the protoplasts of an individual are alike in sexual equipment, and, as a consequence, individuals are sexually differentiated. Finally, with the appearance of heterospory, sexual individuals are permanently differentiated.

Apparently, the amount of available nutrition holds no relation to the differentiation of sex, except as it inhibits the production of highly nutritive eggs by a body of small nutritive capacity, and at the same time permits the production of sperms. In other words, nutrition does not determine sexuality, but sometimes determines the opportunity for the expression of sexuality.

All sporophytes contain both sex-determiners, and in sporogenesis they are transmitted to the spores, which may produce bisexual gametophytes or unisexual gametophytes, dependent upon the distribution of the inhibitors.

All fertilized eggs contain both sex-determiners and inhibitors, and may transmit them all to the sporophyte, in which case the sporophyte will produce spores functioning alike, or two kinds of spores, differing in their inhibitors.

In the case of the "dioecious" sporophytes of seed plants, a fertilized egg transmits to the sporophyte only one inhibitor, which determines whether it produces megaspores or microspores.

The presence of sex-determiners and sex-inhibitors determines not only the character of the gamete produced, but also the character of the sexual structures associated with it; and in the case of dioecious sporophytes determines the development of a much wider range of structures than the appropriate sex organs.

CHAPTER VII

PARTHENOGENESIS

By parthenogenesis is meant the germination of an unfertilized egg. This phenomenon is not peculiar to any region of the plant kingdom, but may occur in any group. A few illustrations will present the facts.

In the water molds (*Saprolegnia*) parthenogenesis is very common. All stages in the abortion of the male organ (antheridium) are found, and still the eggs seem to germinate as freely as if fertilized; in fact, in some species it is a question whether fertilization ever occurs. It will be remembered that in describing the origin of gametes from swimming spores, as illustrated by *Ulothrix*, it was stated that the smaller the spores become the slower is the germination, and the smaller are the filaments produced; until finally spores are reached so small that they are ordinarily incapable of germination. Only exceptionally do they produce very dwarf filaments. It seems to be clear that in this case there is some connection between the nutritive capacity of the spore and its ability to germinate. It is these incapable spores that become gametes by some physiological change that determines pairing and fusion. It is reasonable to suppose that if these incapable spores were to become large, they would regain the power of independent germination. This is just what happens in the differentiation of gametes in size, the egg regaining all the bulk of the ancestral spore and more. There seems to be no obvious reason, therefore, why the unfertilized

eggs of *Saprolegnia* should not be as able to produce new individuals as unfertilized spores, if germination is related in any way to nutritive capacity. For the same reason one would not expect sperms to germinate.

That parthenogenesis occurs at all shows that the presence of sexual characters, whatever they may be, does not necessarily inhibit germination in the absence of fertilization. Of course we can only assume that the parthenogenetic eggs of *Saprolegnia* resemble in every particular those that are not parthenogenetic. The inference is that while the usual stimulus to the egg that starts the germination is applied by the sperm, this stimulus may be applied also in other ways. It must not be forgotten that a spore is simply a freed protoplast and that any vigorous protoplast may produce a new individual. Parthenogenesis, therefore, seems to be a very natural phenomenon. It is surprising that it is not more common among plants; in fact, it is probably much more common than is realized. Certain species of *Ectocarpus*, a genus of brown seaweeds, indicate that eggs and sperms have the same power of germination. In some of the gametangia (or sporangia) the swimming spores function either as spores or as gametes; while in others in which the spores are of several sizes, the largest ones may function either as eggs or as spores. In both of these cases spores may function as gametes; but if one should reverse the statement and say that occasionally a gamete functions as a spore, it would be a case of parthenogenesis.

While it seems easy to explain why such a vigorous protoplast as the egg should be able to germinate without fertilization, thus behaving as a spore, the complication

that parthenogenesis introduces is connected with the alternation of generations, involving as that does an alternation in the number of chromosomes. In alternation of generations the fertilized egg, necessarily containing the double number of chromosomes, produces a $2x$ structure, the sporophyte. When the sporophyte produces spores, the reduction in the number of chromosomes occurs, so that the spore is an x cell, which produces an x structure, the gametophyte. The sporophyte, therefore, is characteristically $2x$, and the gametophyte is just as characteristically x. When parthenogenesis occurs, it would be natural to expect that the egg will produce an x structure, because there has been no fertilization to double the number, and still it produces a sporophyte, just as though it were a fertilized egg with the double number of chromosomes. Is this parthenogenetically produced sporophyte really an x structure; and if so, is the number of chromosomes a necessary feature of a sporophyte or a gametophyte? Is a structure a sporophyte because it is $2x$, or because it is produced by an egg and produces spores? In case an x sporophyte is developed from a parthenogenetic egg, there is no reduction in spore-formation, and there is no change in the number of chromosomes throughout the life history. In other words, the egg acts as a spore produced by the gametophyte, but in all other respects the two generations maintain their differential features.

The ferns may be used as illustrations of this situation. They are notoriously apogamous, which means that the gametophyte (prothallium) produces sporophytes without the sex act. Of course apogamy includes parthenogenesis, which is apogamy in which the unfertilized egg

produces a sporophyte; but it includes much more, for apparently almost any cell of the gametophyte may produce a sporophyte. This production of sporophytes by vegetative cells is called "vegetative apogamy" to distinguish it from parthenogenesis. This miscellaneous production of sporophytes by the gametophyte is an impressive illustration of the fact that any vigorous protoplast under appropriate conditions can produce a new individual. One would suppose, however, that in this case the new individual would be another gametophyte, developed vegetatively from the old one. Attempts have been made to explain the vegetative production of a sporophyte by a gametophyte, by assuming that the chromosomes have been doubled in some way by vegetative fusion. However, careful cytological studies have shown that x sporophytes do arise apogamously from fern prothallia. If a fertilized egg invariably produces a sporophyte, it is because it contains sporophyte determiners, and there is no reason why an unfertilized egg should not contain the same. The situation is not so clear in the case of vegetative apogamy, but any protoplast that functions as an egg must have received the sporophyte determiners. The function of an egg in a life history, therefore, seems to be to produce a sporophyte, and any protoplast, whether a fertilized egg, an unfertilized egg, a spore, or a vegetative protoplast, that produces a sporophyte, does so because it has received the sporophyte determiners, and is thereby an egg in function.

In ferns apospory is also a common phenomenon, which means that the sporophyte produces gametophytes without using spores; that is, a gametophyte buds

out directly from a sporophyte. The problem is the same in this case as in apogamy. If the sporophyte is the usual $2x$ structure, it would follow that the aposporously produced gametophytes are $2x$, and that the reduction would probably occur in connection with gamete-formation. In fact, in all investigated cases where spores have been eliminated in the life history, the reduction occurs in connection with gamete-formation. If the sporophyte has been produced apogamously, its vegetative cells would probably be x and the aposporous gametophytes would contain the usual x number. Therefore, any protoplast of a sporophyte, whether a spore or a vegetative cell, can produce a gametophyte, and must therefore contain gametophyte determiners. On the other hand, it will appear later that any vegetative cell of a sporophyte may produce another sporophyte; that is, it may function as an egg. It is evident, therefore, that while spores are restricted to gametophyte-formation, and eggs to sporophyte-formation, undifferentiated protoplasts may become either spores or eggs in function. There seems to be no escape from the conclusion that the determiners for both sporophyte and gametophyte exist in the cells of both generations, and that in both generations protoplasts may function either as spores or eggs. It is also evident that while the sporophyte is characteristically a $2x$ structure and the gametophyte an x structure, the number of chromosomes is not one of the determiners.

The cases of parthenogenesis among seed plants illustrate some additional features of apogamy in general and parthenogenesis in particular. A few cases of parthenogensis among seed plants were reported many

years ago, but these have since turned out to be either vegetative apogamy or sporophytic budding. More recently, many real cases of parthenogenesis have come to light in various groups of seed plants, and they seem to be particularly numerous in the highest family, Compositae, to which sunflowers, asters, dandelions, etc., belong. It is now known definitely that in many cases the embryo of seed plants is produced by an unfertilized egg. It will be recalled that fertilization in seed plants is preceded by pollination, that is, the transfer of pollen from the stamen to the receptive surface of the pistil, usually of another flower; by the growth of the pollen tube from the surface of the pistil to the ovule within, and through the ovule to the cavity (embryo sac) containing the egg; and then by the discharge of sperms into the embryo sac. There are many chances that this long program may fail at some point, and it is doubtless true that parthenogenesis is far more common among seed plants than is generally supposed.

Some of the best known cases have been subjected to careful cytological investigation and a remarkable fact has been discovered. In every case examined the parthenogenetic egg was *2x;* that is, it contained the sporophyte number of chromosomes rather than the gametophyte number. In other words, it contained the number of chromosomes that belong to a fertilized egg. This could point to but one conclusion, fully confirmed by observation, namely, that the reduction divisions had not occurred in spore-formation, so that the spores were *2x*, and therefore produced *2x* gametophytes. This led to the question whether a *2x* cell can be regarded as an egg in the ordinary sense. In any event, it indicates

that parthenogenesis may depend, not so much upon the peculiar behavior of an unfertilized egg, as upon the failure of the reduction division. In this case the double number of chromosomes runs continuously throughout the life history, being the same in both gametophyte and sporophyte.

The embryo sac of the flowering plants (angiosperms) contains one egg, and yet in many cases more than one embryo is formed. In orange seeds, for example, it is very common to find more than one embryo; and in a recorded case of a species of onion, referred to in a preceding chapter, five embryos were found in a single sac. This phenomenon is called *polyembryony*, and it deserves analysis. In the case of the onion referred to, the embryos had three different origins: one embryo from the fertilized egg; three from other cells of the gametophyte within the embryo sac; and one from a cell of the tissue surrounding the embryo sac. The three embryos from cells of the gametophyte other than the egg would be cases of vegetative apogamy, as in the ferns described above; but the tissue about the embryo sac belongs to the parent sporophyte, and therefore the embryo produced by it was not even a case of vegetative apogamy, but was a sporophyte produced directly by another sporophyte; in other words, what is called sporophytic budding. This is an excellent illustration of the fact that the usual results of fertilization, so far as the production of the sporophyte embryo is concerned, can be obtained from almost any cell. It shows further that while in cases of apospory vegetative cells of a fern sporophyte may produce gametophytes directly, the vegetative cell of a sporophyte may produce another

sporophyte directly. This is vegetative multiplication, the most primitive method of reproduction, common in seed plants which reproduce by tubers, bulbs, etc. The case of the onion cited is interesting also as an illustration of the occurrence of all three methods of reproduction simultaneously, and all resulting in the same product, a sporophyte embryo. Sexual reproduction is represented by the fertilized egg; the three other free cells of the gametophyte behave like spores; while the cell of the adjacent tissue produces an embryo vegetatively.

An additional fact in reference to parthenogenesis in flowering plants has been secured recently. A plant known to be parthenogenetic was shown to have $2x$ eggs; but it was also known to be pollinated, and its sperms were seen discharged into the embryo sac. Moreover, the sperms contained the x number of chromosomes and were apparently functional in every particular; and yet, although a sperm frequently came into contact with an egg, there was no fusion, that is, no fertilization. It seems to be established, therefore, that a $2x$ egg is incapable of fertilization, and must germinate parthenogenetically or not at all. This cannot have anything to do with the actual number of chromosomes, for plants with very different numbers may cross freely. It is evident that if a $2x$ egg is incapable of fertilization, it is because some physiological change accompanies the reduction division which favors fertilization. It would seem, therefore, that the sexual characteristics are developed at the reduction division, even when a gametophyte body intervenes between the reduction division and the gametes.

The facts presented above suggest certain conclusions in reference to parthenogenesis.

(1) An egg may function as a spore, in that it may germinate without fertilization.

(2) It seems evident, however, that an egg so differs from a spore in constitution that it needs a different kind of stimulus for germination.

(3) Usually this stimulus is applied in connection with the act of fertilization, but it can be applied in some other way.

(4) The peculiar organization of the egg for fertilization is determined at the reduction division.

(5) If the reduction division does not occur, parthenogenesis is more likely to occur, and the egg is probably incapable of fertilization.

(6) If the spores are eliminated from the life history, as in animals and some plants, reduction occurs in connection with gamete-formation, and the gametes are the only x cells, being the only representatives of the gametophytes.

(7) An egg necessarily produces a sporophyte, and a spore a gametophyte, but vegetative protoplasts of either generation may be organized to produce either generation; that is, they may function as eggs or spores, dependent upon the determiners they have received.

(8) The number of chromosomes contained by a reproductive cell does not determine which generation it will produce, for both x and $2x$ protoplasts produce either sporophytes or gametophytes.

(9) In general, therefore, parthenogenesis differs from reproduction by other protoplasts only in requiring a more specific stimulus, a fact which ordinarily prevents eggs from germinating unless fertilized.

CHAPTER VIII

A THEORY OF SEX

In the preceding chapters an attempt has been made to state the principal facts connected with sexuality among plants, with such illustrations as might indicate the variety of sexual phenomena. The facts are numerous, and in some instances may seem to be contradictory, but they are all consistent with some general situation that determines sexuality. A review of the more prominent facts not only will serve the purpose of a summary freed from confusing details, but also may suggest a working hypothesis.

The first appearance of gametes is so closely associated with spore-formation that they appear to be only swimming spores greatly reduced in size. This impression is confirmed by the fact that occasionally such gametes function as spores, but their germination is slow and the product is a dwarf. There are three features belonging to these primitive gametes that deserve consideration: they are motile, very small, and pairing cells.

It is obvious that motility is not an essential feature of sexual cells, for soon one of the pairing gametes becomes non-motile, and finally both of them are non-motile. Motility, therefore, is a secondary feature, common to both gametes at first, retained with remarkable persistence by the male gamete, but dispensed with entirely in most seed plants. It is a mechanical device that aids in making pairing possible, and holds no more

relation to sexuality than do the swimming appendages of spores to their germination.

It is equally evident that the small size of these primitive gametes, as compared with the spores of the same plant, is not an essential feature of sexual cells. In other words, they are not gametes simply because they are smaller than the spores. Later, one of the pairing gametes, the egg, becomes much larger than the spores, and still it is a gamete. When the primitive gametes and spores are contrasted, and also the sperm and egg, it is discovered that the difference in size is due chiefly to the difference in the amount of cytoplasm. Moreover, in some seed plants the functioning sperm has no cytoplasm at all. This variation in the amount of cytoplasm, and its complete elimination in some cases, indicates that the amount of cytoplasm is also a secondary feature of sexual cells, and therefore the differences in the size of gametes may be eliminated from the fundamental problem of sex. So far as evidence is available, cytoplasm is responsible chiefly for the nutritive supplies of ordinary cells, and at least one of its functions in connection with sexuality is probably to supply nutrition for the sex act and its product, nutrition that may be supplied in some other way.

Another important function of the cytoplasm of the egg has been described by Lillie. He has discovered that as the egg matures there appears in the cytoplasm a substance necessarily related to the act of fertilization. This substance is produced at a certain stage in the development of the egg, and at that stage fertilization can occur; but it is not effective long, so that if a particular period in the history of the egg is passed, fertilization

cannot occur, just as it cannot occur before this physiological moment. If this substance is present in the egg, the contact of the appropriate sperm stimulates it into activity, and the machinery of fertilization is put in motion. It should be recognized, however, that even this important "activating" substance is not an essential feature of sexuality, but belongs to the category which includes a number of secondary features that aid in making the sex act possible.

The third feature of the primitive gametes, namely, that they are pairing cells, is certainly a feature that belongs to all gametes, and yet there are pairing and fusing cells that are not gametes. For example, in the embryo sac of angiosperms there is a single egg which pairs with a sperm, but there is always also another pairing and fusion, resulting in the cell that produces endosperm. This cell is a case of triple fusion, three nuclei uniting to form the primary endosperm nucleus. In some cases more than three nuclei fuse to form the endosperm nucleus. Moreover, the endosperm in the course of its formation may show cell fusions which certainly do not represent sex acts. Through all the great groups of plants such fusions occur, and it is evident that pairing and fusing are not peculiar to gametes, and therefore do not represent the essential feature of sexuality. Pairing seems to be a secondary feature, just as are motility and cytoplasm, and it represents a mutual attraction that makes the sex act possible, just as motility is a mechanism that makes pairing possible. This mutual attraction is certainly due to contrasting chemical compounds or physical conditions which are displayed by other cells as well. Moreover, when the gametes

are brought together by other secondary apparatus, as in the case of a discharge of a sperm from a pollen tube into the embryo sac of an angiosperm, the mutual attraction seems to be reduced to a minimum, and yet the sex act and its results are just as vigorous as ever.

It is certainly true that the primitive gametes differ from the spores with which they are so closely associated in pairing and fusing, and this difference must be accounted for first. It will be remembered that these gametes are produced by just such vegetative protoplasts as produce spores, except that they are produced later in the vegetative history of the plant than are the spores. In general, gamete-production in these primitive plants represents their last performance, when vegetative activity is rapidly declining. Spores are formed in conditions of greater activity, and the result is different. It follows, therefore, that the difference in result is due to a difference in the activities of the protoplast in the two cases, a difference associated with declining vigor. Under such conditions it is not only conceivable, but obvious, that the products of metabolism will differ, and that substances will be produced that do not appear when the protoplast is in full activity. This means that the gametes will contain substances that the spores do not, and among these substances are those that determine the mutual attraction that results in pairing. If this is true, it follows that different substances differentiate gametes into two kinds that are mutually attractive. This differentiation may occur among the gametes produced by a single protoplast, but soon it more commonly distinguishes the gametes

produced by different protoplasts. These characteristic substances which appear late in the vegetative history of plants may be regarded as among the end products of waning metabolism.

We are familiar with just such a situation in the autumnal coloration of leaves, where waning metabolic activity results in products entirely new, among which is the one that gives the characteristic red coloration. It does not follow that these substances which characterize gametes appear only when the vegetative vigor of the plant as a whole is declining. This is generally true of such plants as the filamentous algae, used to illustrate primitive gametes, but in more complex plants, living in different conditions, this decline of metabolic activity may occur in a region of the plant body rather than in the body as a whole. In other words, it is the condition of the individual protoplast rather than of the body as a whole which determines the appearance of these gametic substances.

In the mosses, for example, sex organs are produced by a body evidently vigorous, a body which may continue active through a subsequent season. It is usually stated that the developing sex organs of mosses, which appear at the tips of branches or of the main axis, check the growth of the axis. It is a fair question to ask whether the sex organs do not appear because for some other reason growth has been checked. A checked growth indicates declining vegetative vigor, and this favors gamete-formation. The conclusion seems reasonable, therefore, that as vegetative vigor declines the metabolism of the plant produces substances that are characteristic of gametes, and that this gamete-formation

may be favored in a simple plant body as a whole, and in a complex plant in some definite region of the body.

Evidence that gamete-formation is associated with relatively feeble metabolism may be obtained from other illustrations of another kind than those just cited. If gametes are produced under conditions of waning vegetative activity, it follows that zygotes are formed under conditions unfavorable to germination. As a consequence, they usually pass into a dormant and protected stage until vegetative conditions begin to be favorable again. The protection may be given by a zygote wall or by surrounding structures, but delay in germination is necessitated by the conditions in which the zygotes are formed. A retracing of the steps which bring vegetative activity to a close is often observed in the beginning of vegetative activity at the opening of the next vegetative season. When a fern spore germinates, metabolism begins in a relatively feeble way, and during this early period antheridia are formed, often in great abundance. Later, when the development of the prothallium becomes more vigorous, sperm-formation ceases. The so-called "inhibitor" of sperms in this case, therefore, is the disappearance of the characteristic substances that belong to gametes on account of the increased vegetative activity of the protoplasts. In this case only such gametes can be formed as are characterized by a small amount of cytoplasm. Later in the history of the fern prothallium, after it has developed a well-nourished body, cells in the apical region become checked in vegetative activity, the substance characteristic of gametes appears again, and eggs are developed.

If gametes were the only cells that pair and fuse, no further explanation of sexuality would seem necessary, but, with other cell fusions occurring, a distinction must be made. In many cell fusions the cytoplasms only are involved, the nuclei remaining distinct. Since it is well established that sexual fusion is essentially a fusion of nuclei, such cases do not obscure the problem. There are many cases of nuclear fusion, however, which do not appear to be sexual fusion, and these obscure the problem seriously. It is entirely possible that all nuclear fusions represent sexual fusions whose results are obscured in some way. This would be the easiest way of disposing of the difficulty, for in this case any pairing cells resulting in nuclear fusion would represent sexual cells, and these could be differentiated from all other cells by containing the mutually attractive substances. But such an escape from the difficulty is hardly justifiable, and a further explanation is necessary.

The nuclear fusion referred to as occurring in the angiosperm embryo sac, in which a sperm fuses with cells that are not eggs, is regarded by many as a real sexual fusion. In fact, the occurrence of the two fusions of sperms in the embryo sac, one with the egg and the other with the endosperm nucleus, is usually called "double fertilization." This case may be waived as still within the region of discussion, but certainly the result of this debated nuclear fusion is not at all the result that follows the sex act. The nuclear fusion that occurs in connection with spore-formation in the Ascomycetes has been regarded as a sexual fusion, but, if so, there would be two separate sex acts in the life histories of certain Ascomycetes, which would introduce us to a

still more difficult problem. But there remain cases of nuclear fusion which cannot be disposed of as being under discussion. For example, in endosperm-formation in gymnosperms and angiosperms, nuclear fusions are frequent in what is evidently simple growing vegetative tissue. This must mean that such cells contain the substances described as characteristic of gametes, and they determine their pairing and fusing; and if these substances are produced in connection with enfeebled metabolism, then such nuclear fusions as occur in connection with endosperm-formation indicate a relatively low grade of vegetative vigor. It would follow that such fusions might occur at any time in connection with feeble or waning metabolism.

If pairing and nuclear fusion are not peculiar to gametes, although universally displayed by them, what is the essential feature? The only answer that can be made is that gametes are pairing cells whose nuclear fusion results in the production of a new individual. This means that in addition to possessing mutually attractive substances formed in connection with low metabolism, gametes possess nuclei so constructed that when the two fuse a new individual is initiated. This does not mean that neither gamete can produce a new individual alone, for parthenogenesis would contradict this. It means a new individual can only be produced after the nuclei have fused. In other words, the essential feature of sexuality must lie in the peculiar structure of the nuclei of the sexual cells. Whether this peculiar structure is chemical or physical or both, must be a matter of opinion based on no direct evidence. It is reasonable to suppose that it is a problem belonging to

the overlapping regions of physics and chemistry. Nor can it be true that gametes are peculiar in containing the factors of heredity, for these must have been handed down through all the cell generations leading to the gametes. Gametes furnish the opportunity for heredity to express itself, but so do spores, and so does vegetative multiplication.

If gametes are peculiar in the construction of their nuclei, how do they develop this peculiarity? The evidence given in the preceding chapters seems to make it clear that this gametic peculiarity, whatever it may be, is developed in connection with the reduction division. Among plants this division occurs generally in connection with spore-formation, and when there are no spores, as in *Fucus*, it occurs in connection with gamete-formation, as in animals. In case the reduction division fails in connection with spore-formation, it has been observed that the resulting $2x$ egg is unable to fuse with the sperm. If fusion is made possible by the presence of the mutually attractive substances referred to, it would seem that these also may be developed in connection with the reduction division. In any event, the reduction division determines the sexual condition, and the peculiarity of this division as compared with ordinary division is related to the peculiar constitution of the nuclei of gametes as compared with other nuclei. If gametes have any structural peculiarity, it must be developed in connection with this peculiar nuclear division. In well-balanced alternation of generations, as in bryophytes and pteridophytes, there are many cell generations between spores and gametes, and how the peculiarities of the gametes are transmitted through

the cell generations of the gametophyte is a subject of speculation, but certainly something maintains a continuity between spores and gametes. In heterosporous plants, chiefly the seed plants, the cell generations between spore and gamete become fewer and fewer, until finally the sperms are reached in two successive cell divisions, and the eggs are reached in two or three successive divisions. The next advance would be the elimination of spores entirely and the occurrence of reduction in connection with gamete-formation, as in animals.

An interesting situation is presented by *Coleochaete*, a green alga. The zygote in germination produces a spore-case, which for a long time was thought to be a sporophyte with the $2x$ number of chromosomes, as it certainly is a sporophyte in function. It is now found that when the $2x$ zygote divides, the reduction division occurs, so that the spore-case is an x structure. The result is that the zygote is the only $2x$ cell in the life history. However, since this spore-case is also a mass of sporogenous cells, the reduction division occurs very shortly before its usual occurrence in connection with spore-formation. In *Coleochaete*, therefore, the cell generations extending between the reduction division and gamete-formation include the whole life history of the plant.

In conclusion, the impression one obtains of sexuality as a method of reproduction is that it represents protoplasts engaged in reproduction under peculiar difficulties that do not obtain in reproduction by spores or by vegetative multiplication, and that its significance lies in the fact that it makes organic evolution more rapid and far more varied.

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